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Cover: Illustration of *Apomys datae*, based on specimens from Mt. Bali-it, Balbalasang, Kalinga Province, Luzon. (Drawing by Velizar Simeonovski.)

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Preface

> "*Since [publication of 'Geographical Distribution of Animals,'] … considerable additions have been made to [the] fauna [of the Philippines], and these have the effect of diminishing their isolation from the other islands…. This brings the known mammalia to twenty-one species, and no doubt several others remain to be discovered.*" (Wallace, 1880, pp. 354–355).

> "*The Philippine Islands, however rich in birds, have always previously been looked upon as a group very poor in Mammals, especially … in regard to really peculiar indigenous Mammals…. But in the great northern island of the group, Mr. Whitehead has made a most wonderful and unexpected discovery, that of a new and peculiar Mammal-fauna…. Science is to be congratulated on the wonderful series of new forms….*" (Thomas, 1898, pg. 377).

> "*There is an impression among mammalogists and biogeographers that the native Philippine rats are well known, especially that spectacular segment of the fauna that lives on the western highlands in northern Luzon (Thomas, 1898). This is not so. The natural history of nearly all the native species is either unknown or encapsulated in sketchy descriptions made by collectors…. The diversity of the fauna, at the level of genera and species, is greater than generally realized.*" (Musser, 1982, pg. 1)

When Alfred Russel Wallace published his great volume *Island Life* in 1880, he was already well established as the "father of biogeography" through his own field studies in South America and the Indo-Australian region and his massive compilation and analysis of data produced by biologists around the world. His enumeration of the Philippine mammal fauna as including 21 species, plus "several others remain[ing] to be discovered," led to his description of the islands as having a "comparative poverty of species" (Wallace, 1880, pg. 355). John Whitehead's discovery, less than two decades later, of six new genera and eight new species from a single mountain in northern Luzon (Mt. Data), plus several additional genera and species from other islands in the Philippines, must have astounded biologists every bit as much as implied by the second quote above from Oldfield Thomas, a British biologist not given to overstatement. It was, quite simply, utterly unexpected.

Studies of Philippine mammals during the following two decades, exemplified by Miller's (1910) description of two new genera and 16 new species in a single publication, demonstrated that the potential for startling new discoveries remained great. Previously unknown species continued to be found on a frequent basis through the 1920s, and one of the most extensive expeditions, undertaken in 1946–47, produced seven new species (based on current taxonomy; Sanborn, 1952), one of which was later considered to represent a new genus. But the rate of discovery declined rapidly thereafter, with few species described from 1952 to the early 1980s. Mammalian diversity in the Philippines, it seemed, had come to be well known, with a limited number of surprises awaiting further studies.

It was this assessment of the fauna as "well-known" to which Musser (1982) responded with the third quote above. Musser went on to describe three new genera and nine new species from the Philippines during the 1980s and 1990s, in each publication emphasizing that great discoveries awaited anyone who conducted research in the archipelago, through both discovery of previously unknown taxa and developing new perspectives on the ecology of this highly distinctive fauna.

Musser's comments have proven to be prophetic: the Philippine archipelago remains a place where remarkable new mammals are being discovered. In this volume, a new subgenus and seven species of the genus *Apomys* are described, following quickly on the heels of the description of a new genus of mouse (*Musseromys*; Heaney et al., 2009), and recent descriptions of new species of the endemic rodent genera *Apomys*, *Archboldomys*, *Batomys*, *Chrotomys*, and *Rhynchomys* (Rickart et al., 1998, 2005; Balete et al., 2006, 2007, 2008; Heaney & Tabaranza, 2006), two new shrews (*Crocidura panayensis* and *C. batakorum*; Hutterer, 2007), and three new bats (*Desmalopex microleucopterus, Dyacopterus rickarti,* and *Styloctenium mindorensis*; Esselstyn, 2007; Helgen et al., 2007; Esselstyn et al., 2008). Furthermore, for the first time, the evolutionary diversification of the fauna is being made clear (Steppan et al., 2003; Jansa et al., 2006; Esselstyn & Brown, 2008), showing that not only are many genera unique to the Philippines, but also that many of these genera are in turn members of endemic clades—entire branches of the tree of life that are found nowhere else on earth.

It is remarkable that, until recently, the great majority of what was known about the mammalian fauna of Luzon—the largest island in the Philippines—was limited to fairly extensive collections from just two places: the Central Cordillera and Mt. Isarog (see fig. 3 in Heaney et al., this volume). In 2000, contributors to this volume began a series of intensive, standardized surveys of mammals on each of the many mountain ranges and isolated mountains on Luzon. The first, in the northern portion of the Central Cordillera, provided the first extensive and quantitative assessment of mammalian community variation along an elevational gradient in those mountains (Rickart et al., 2011). Another, conducted in the Zambales Range of west-central Luzon, was the first extensive, detailed survey of that area (Balete et al., 2009) and yielded a new species of *Rhynchomys* and two species of *Apomys* described by Heaney et al. (this volume). Several brief, preliminary surveys in the Sierra Madre (Duya et al., 2007), coupled with the detailed survey of Mt. Cetaceo in that same range (Duya et al., this volume), present the first clear picture of the mammalian fauna of the longest range on Luzon. Together, the Central Cordillera, Zambales Range, and Sierra Madre represent the three largest mountain ranges on Luzon, and the locations of much of the endemic mammalian diversity.

In this volume, we further extend our coverage of Luzon with the results of a thorough survey of the mammals of the Mingan Mountains (see fig. 3 in Heaney et al., this volume), a small range for which there were previously no data on mammals (Balete et al., this volume). This yielded two endemic species of *Apomys* described here (Heaney et al., this volume), and apparently new (though still undescribed) species of *Archboldomys* and *Rhynchomys* as well. We also provide the results of a survey of the mammals of Mt. Palali, the highest peak in the Caraballo Mountains (Alviola et al., this volume), a fairly large range that lies between the Central Cordillera and the Sierra Madre. It is noteworthy that the mammals of this range appear to include a mixture of species from the Central Cordillera and the Sierra Madre, although further taxonomic studies are needed. The papers in this volume thus represent a substantial advance in our knowledge of the mammals of Luzon, but do not represent the end point. The results from our recent surveys in the southern Sierra Madre and on Mt. Banahaw, Mt. Labo, and Mt. Natib await our attention and will be published in due course. At that point, data will be available on all of the likely areas of mammalian endemism on Luzon, providing, for the first time, the opportunity to document thoroughly the biogeography of the nonflying mammals of this largest and most geographically complex of the Philippine islands.

However, as noted in several of the chapters in this volume, the insectivorous bats are often the least thoroughly sampled portion of the fauna. In that regard, the contribution by Sedlock et al. (this volume) is especially important because it not only yielded detailed information on bats from Mt. Banahaw, but provides a crucial point of reference for gauging the effectiveness of insectivorous bat surveys done elsewhere and makes it clear that much research remains to be done on this highly diverse portion of the mammal fauna.

All of these discoveries have important consequences for conservation planning and management in the Philippines. The surveys reported in this volume demonstrate that the Mingan Mountains and the Zambales Mountains each have several endemic species, but neither has a designated protected area despite being deserving of them. Other species described here from Mt. Banahaw and Mt. Cetaceo reinforce the importance of Mt. Banahaw–San Cristobal National Park (Sedlock et al., this volume) and the Northern Sierra Madre Natural Park (along with Mt. Cetaceo; Duya et al., this volume) for protecting the biodiversity heritage of the Philippines. The survey of Mt. Palali, in the Caraballos Mountains (Alviola et al., this volume), provides the first substantial and quantitative data on the mammals of that region. The data provided for each of these areas will have substantial utility for effective management of the areas, since it is now clearer which species are most vulnerable and which habitats are most crucial for protecting endemic mammalian biodiversity. Additionally, the chapters included here point the way toward a phase of discovery among insectivorous bats that could ultimately equal the recent discoveries among nonflying small mammals.

Clearly, we live in an age of discovery. New species and, at times, new genera continue to be discovered, and researchers are rising to the challenge posed by Musser in 1982—to document the natural history of this remarkable fauna so the story of its historical development can be told clearly and accurately. Understanding the means by which the Philippine archipelago has come to possess one of the world's greatest concentrations of unique biodiversity requires that we know not only of the existence of all species, but also their history of diversification and their ecology. Development of this broad-scale and integrated view of the mammalian fauna has begun and shows the potential for the Philippines to become one of the premier examples of the evolutionary origin, ecology, and effective conservation of biodiversity in oceanic archipelagoes.

Each of the chapters that follows acknowledges the many people who have made possible the individual studies, but we give special thanks here to the Philippine Department of the Environment and Natural Resources for all they have done to support and encourage our research at all of our study sites. We especially thank Dr. T. Mundita Lim, T. Manila, J. DeLeon, C. Custodio, M. Mendoza, and A. Tagtag at the Protected Areas and Wildlife Bureau for their continuing support. The collaboration of the Field Museum with Conservation International–Philippines, the National Museum of the Philippines, and the University of the Philippines has added greatly to the productivity of all of our efforts. Preparation of this volume, and much of the field work, has benefited greatly from financial support provided by the Barbara Brown Fund for Mammal Research, the Ellen Thorne Smith Fund, the Marshall Field Fund, and the Negaunee Foundation, for which we are deeply grateful.

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Chapter 1: Seven New Species and a New Subgenus of Forest Mice (Rodentia: Muridae: *Apomys*) from Luzon Island

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Abstract

Surveys of small mammals on carefully selected mountains and mountain ranges on Luzon Island, Philippines, since 2000 have led to the discovery of seven previously unknown species of forest mice, *Apomys*, a remarkable radiation on just a portion of one island. On the basis of morphological and cytochrome (cyt) *b* DNA sequence data presented here, we propose a new subgenus, *Megapomys*, to include the large-bodied members of the genus, which form a monophyletic unit of relatively large mice (averaging ca. 65–110 g) with tails about as long as or slightly shorter than the length of the head and body; all of these species forage on the ground. Other members of the genus are assigned to the subgenus *Apomys*; they are smaller (ca. 18–41 g), have long tails, and usually or often forage above the ground surface. Members of the subgenus *Megapomys* include four previously recognized species (*A. abrae*, *A. datae*, *A. gracilirostris*, and *A. sacobianus*) and the seven new species described here (*A. aurorae*, *A. banahao*, *A. brownorum*, *A. magnus*, *A minganensis*, *A. sierrae*, and *A. zambalensis*). All occur in northern and central Luzon Island, with the exception of one species that occurs on Mindoro Island; none is present in southern Luzon. Each species can be distinguished both morphologically and genetically. Although there are few records of *Megapomys* below 500 m elevation, they are common above about 1000 m, and some species occur near the peaks of the highest mountains on Luzon (i.e., up to nearly 2900 m). On four mountain ranges, two species of the subgenus co-occur, one at lower and one at higher elevations, although there is usually some syntopic overlap. Sister-species usually occur allopatrically in different mountain ranges, with one possible exception. Some of these species occur in areas not previously known to support endemic mammals, indicating that these areas are previously unrecognized areas of mammalian endemism where further study is warranted.

Introduction

With 23 endemic genera of mammals within a land area of ca. 300,000 km^2, the Philippine archipelago has one of the greatest concentrations of unique mammalian diversity of any place on earth (Heaney et al., 1998). Foremost among these in diversity are the murid rodents, with 16 endemic genera and at least 55 endemic species (Heaney et al., 1998; Musser & Carleton, 2005). Previously unknown murids continue to be described (e.g., Rickart et al., 2005; Balete et al., 2006, 2007, 2008; Heaney et al., 2009), many of them discovered recently as part of a continuing effort to conduct a comprehensive survey of the mammals of Luzon Island (e.g., Heaney et al., 1999, 2003; Duya et al., 2007; Balete et al., 2009; Rickart et al., 2011).

The remarkable diversity within the Philippine Muridae resides primarily within two endemic lineages: the "giant cloud rat lineage" (= Phloeomyini *sensu* Lecompte et al., 2008), with five genera and about 15 species (Heaney et al., 1998, 2009; Jansa et al., 2006), and the "earthworm-mouse lineage" (part of the Hydromyini *sensu* Lecompte et al., 2008), with four genera and 22 species by the latest count (Steppan et al., 2003; Musser & Carleton, 2005; Jansa et al., 2006; Rowe et al., 2008). The latter is sister to all Australasian members of Hydromyini (Rowe et al., 2008; Heaney et al., 2009). The most speciose genus among these is *Apomys* Mearns 1905, generally referred to as Philippine forest mice, with 10 species previously described and recognized (Steppan et al., 2003; Musser & Carleton, 2005; Heaney & Tabaranza, 2006). In this paper, we show that past studies have undersampled, and therefore greatly underestimated, the number of species in this genus; herein, we describe seven additional species, all from Luzon. In doing so, we lay a substantial portion of the groundwork

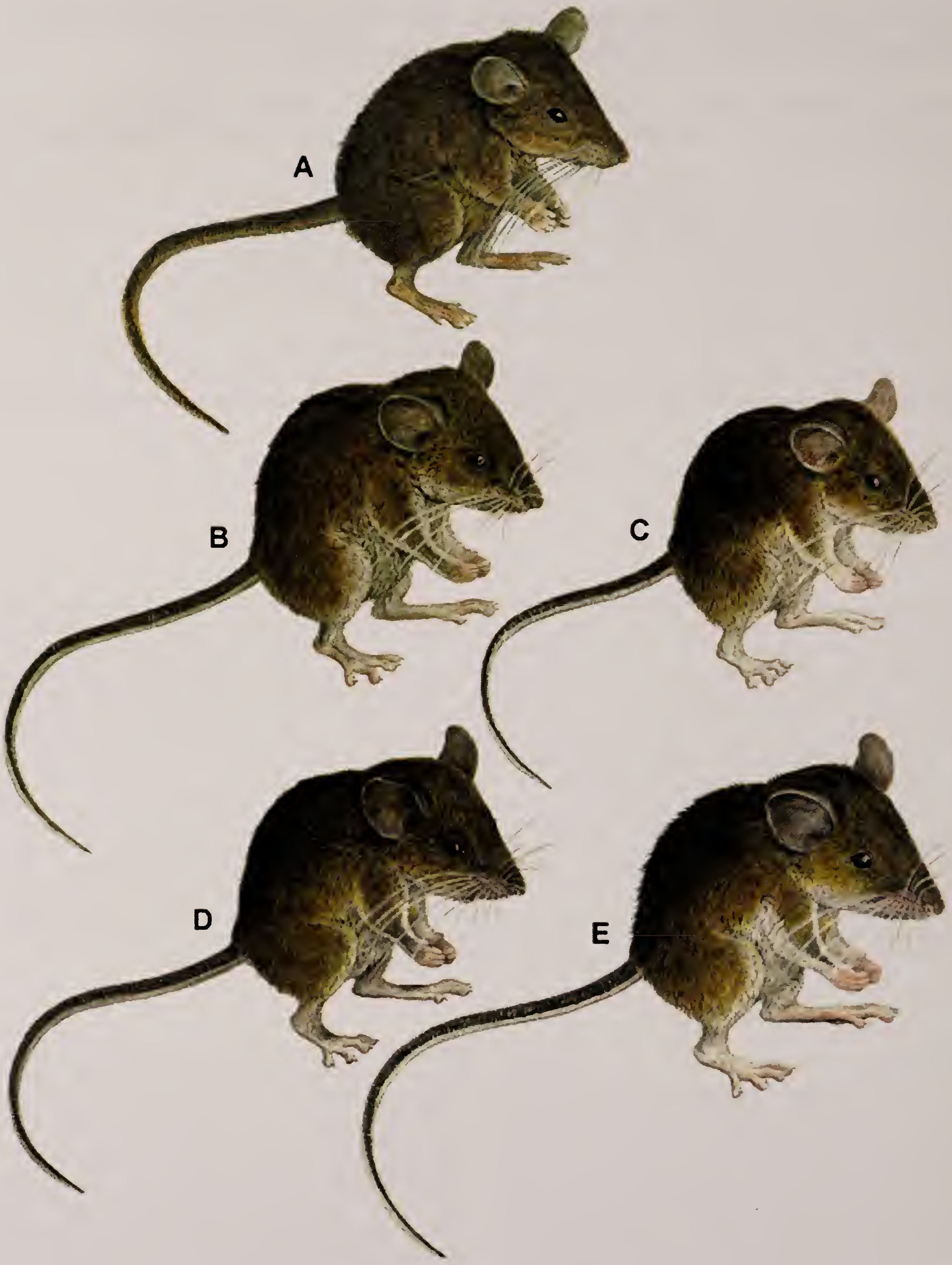


FIG. 1. Color drawings of (**A**) *Apomys gracilirostris*, (**B**) *A. datae*, (**C**) *A. abrae*, (**D**) *A. banahao* sp. nov., and (**E**) *A. magnus* sp. nov. to the same scale. All drawings by Velizar Simeonovski.

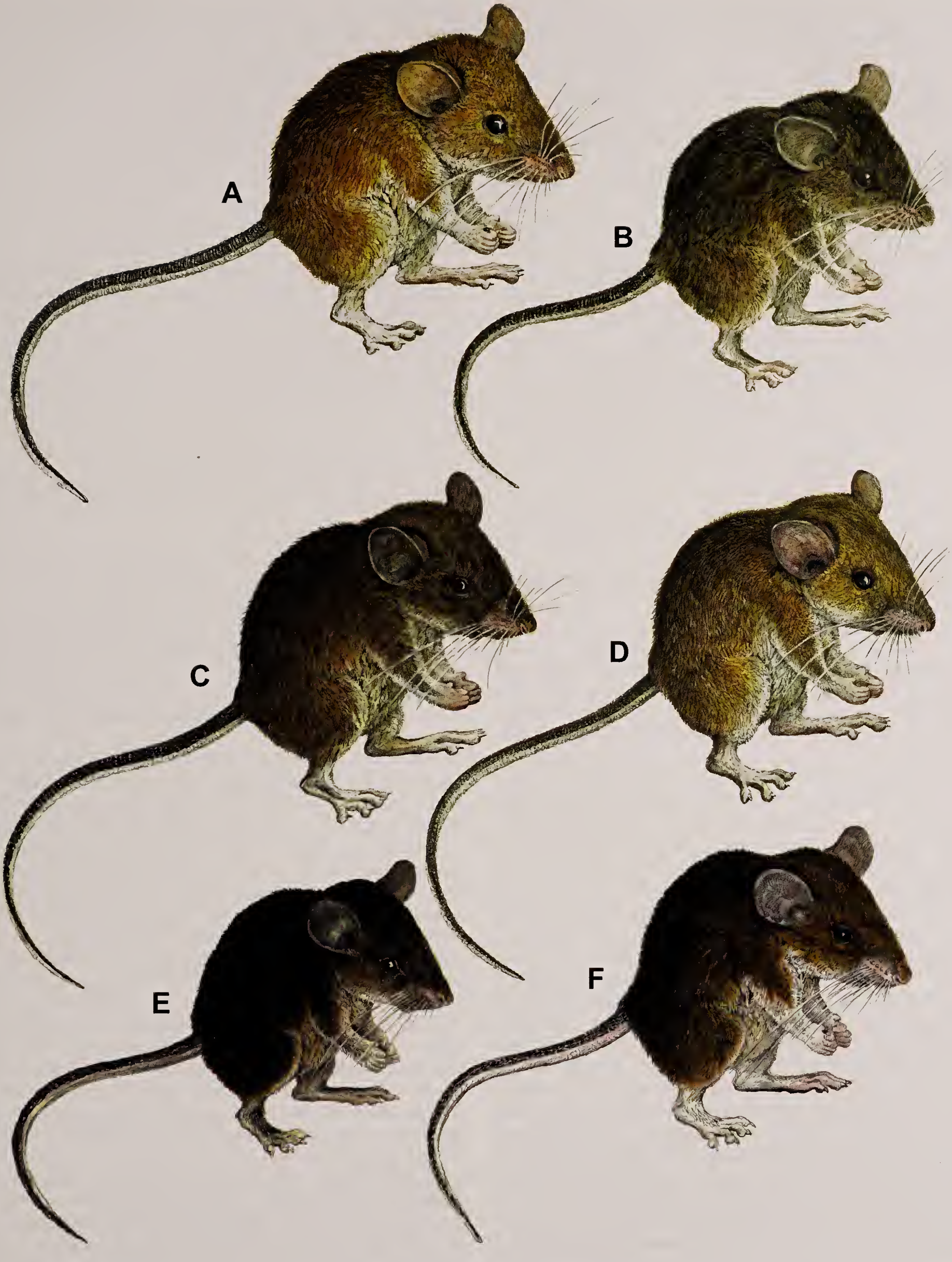


FIG. 2. Color drawings of (**A**) *Apomys zambalensis,* (**B**) *A. brownorum,* (**C** and **D**) *A. sierrae* (from Mt. Cetaceo and Mt. Palali, respectively), (**E**) *A. minganensis*, and (**F**) *A. aurorae* spp. nov., to the same scale. All drawings by Velizar Simeonovski.

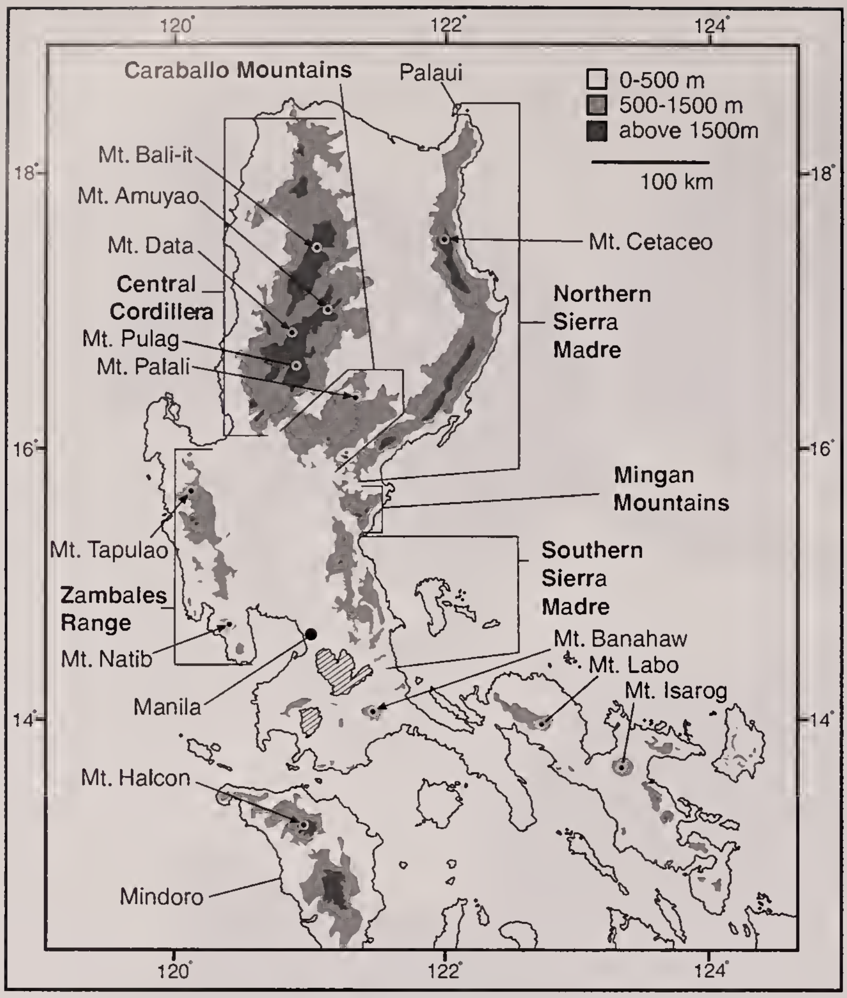


FIG. 3. Map of Luzon and Mindoro, showing mountains and ranges referred to in the text.

for a detailed examination of the geographic patterns of mammalian biodiversity on Luzon Island, the largest island in the Philippines at 102,000 km^2, and the site of remarkable geological and geographical heterogeneity for such limited area.

Mice of the genus *Apomys* occur on most of the oceanic islands of the Philippines, being absent from only three areas: the Palawan region, which is faunistically more closely associated with the Sunda Shelf than with the oceanic Philippines; the Sulu Archipelago, a poorly known but seemingly species-poor set of islands that lie between Mindanao and Borneo; and the small, isolated islands of the Batanes and Babuyan groups that lie in deep water north of Luzon (Musser, 1982; Heaney, 1985, 1986, 2000; Musser & Heaney, 1992; Steppan et al., 2003; Catibog-Sinha & Heaney, 2006; Heaney et al., 2006a). At many of our sampling localities, these mice were the most abundant small mammals, especially at elevations above about 1200 m. As many as four species can occur on a given mountainside, with up to three species occurring syntopically. On Luzon, two ecological groups can be readily identified: small-bodied *Apomys* that forage primarily in vegetation (grass, shrubs, and trees) above the ground, and large-bodied species that forage primarily on the ground (Musser, 1982; Heaney et al., 1998, 1999, 2003, 2006a,b; Steppan et al., 2003; Balete et al., 2009, this volume; Alviola et al., this volume; Rickart et al., 2011).

During the 2004–2006 period of the comprehensive survey of Luzon mammals referred to above, we noted extensive variation in the external morphology of the large-bodied *Apomys* (Figs. 1, 2) that we captured in the northern and central parts of Luzon (Fig. 3), and we subsequently noted consistent cranial variation in parallel with the external morphology. As described below, our mitochondrial gene phylogeny has revealed the presence of clades that corresponded to those morphological units. In this paper, we describe each of these morphologically distinct, genetically monophyletic units as a new species, discuss their patterns of distribution and phylogeny in the context of the previously described species of large-bodied *Apomys*, and consider their distribution patterns within the complex geography of Luzon Island.

Materials and Methods

Specimens examined and/or referred to in this study are housed in the following museums, with their standard acronyms and some "synonyms":

BM(NH)—British Museum (Natural History) = The Natural History Museum (London)
CMNH—Cincinnati Museum of Natural History, Cincinnati, OH
FMNH—Field Museum of Natural History, Chicago = Chicago Museum of Natural History
NMP—National Museum of the Philippines, Manila
USNM—United States National Museum of Natural History, Washington, D.C. = NMNH

For muroid taxonomy and nomenclature, we follow Musser and Carleton (2005) unless otherwise noted.

Heaney examined the holotypes of the following species (housed at the indicated institutions): *Apomys abrae* (FMNH), *A. gracilirostris* (NMP), *A. sacobianus* (USNM), and *A. major* (USNM). We did not examine the holotype of *Apomys datae*, housed at the Staatliches Museum für Tierkunde, Dresden, Germany; for information on this holotype, we relied on Musser (1982).

Most of the specimens obtained during and after 2000 were initially preserved in formalin in the field then rinsed in water and transferred to ethanol. Many have had their skulls removed and cleaned by dermestid beetles, followed by soaking in a dilute ammonia solution, rinsing in water, and picking by hand. Before fixation with formaldehyde, specimens in the field had small amounts of muscle tissue, usually from the thigh, removed and stored in either 90% ethanol or dimethyl sulfoxide (DMSO). Additionally, some specimens were skeletonized in the field, and the skeletons were soaked and stored in ethanol before cleaning by the same procedure for skulls. A few specimens were karyotyped in the field, as detailed below. Once the specimens arrived at FMNH, the tissue samples were stored in the vapor from liquid nitrogen. Older specimens were skinned and stuffed as standard museum study skins in the field, and the skulls were removed and cleaned. Pre-1970 specimens at FMNH had their skulls cleaned by maceration, which sometimes caused teeth to loosen, fall out, or both and cranial sutures to loosen, come apart, or both.

With one exception, uncoated skulls were imaged with an AMRAY 1810 scanning electron microscope (SEM). The specimens were not coated with gold. Because the size of the skulls and mandibles exceeded the photographic frame, SEM photographs were taken of the front, middle, and back of the skull in each view and digitally matched and merged to make the images presented here. The skull of the holotype of *A. sacobianus* was photographed with a digital camera.

Our investigations used qualitative aspects of the external, cranial, and dental morphology; quantitative assessment of mensural craniodental similarities and differences by principal components analysis (PCA); and genetic data. We conducted these studies simultaneously, with the results of each causing us to re-examine and extend our examination of the others. In this paper, we take the results of quantitative morphometric studies as our starting point then present the results from our genetic studies that provide a phylogenetic context generally lacking from the quantitative morphological studies. We also present information on the karyology of four of the species. We follow this with detailed descriptions and comparisons of anatomy for each species, emphasizing the distinctive features that are not captured by measurements. Within the individual species accounts, we also include additional quantitative assessments of craniodental morphometric variation within individual species and among sets of closely related species, and often include bivariate plots to document differences among them and as an aid to identification for future studies.

All specimens collected since 2000 have been prepared and cataloged at FMNH, as described above. Upon completion of this study, approximately half of the specimens will be permanently deposited at the NMP, including all of the holotypes of the species named here. All of the authors of this publication are intended as authors of all species names proposed herein.

Specimens collected before about 1970 often had localities with elevation recorded in feet. Inspection of the elevations indicates that these were estimates, often rounded to the nearest 500 or 1000 feet. We retain these original data in the following text but also provide the elevation converted to meters, rounded to the nearest 100 m for the convenience of the reader.

Measurements and Morphometric Analyses

Measurements of total length (TL), length of tail vertebrae (TV), length of hind foot including claws (HF), length of ear from notch (EAR), and weight in grams (WT) were taken from our field catalogs housed at FMNH or from the tags on older specimens. Our field measurements were taken with plastic rulers graduated to 1 mm or with Pesola scales graduated to 1 g. The length of head and body (HBL) was determined by subtracting length of tail from total length.

Eighteen cranial and dental measurements were taken from individuals, with sample sizes listed in the tables. For our sample, we chose adults that had complete skulls. Adults were defined as those individuals with adult pelage (not the grayer pelage of young animals), cranial sutures (especially the basicranial sutures) fused or nearly so, and molar teeth showing at least moderate wear. Most adult females had enlarged nipples, and most males had testes of relatively large size. Heaney took all cranial measurements with dial calipers graduated to 0.01 mm. The following measurements were taken: basioccipital length (BOL; from anterior edge of premaxillary to posterior edge of occipital condyles); least interorbital breadth (IB); greatest zygomatic breadth (ZB); mastoid breadth (MB); nasal length (NL); length of incisive foramen (LIF); rostral depth (RD; taken from the midpoint of the premaxillary–maxillary suture to the nearest point on the dorsum of the rostrum); rostral length (RL; taken from anteriormost point of orbit to the tip of the nasals); orbitotemporal length (OL; taken from the anteriormost point of the orbit to the posteriormost point of the temporal fossa); alveolar length of maxillary molariform teeth (M^1–M^3); labial palatal breadth at the first upper molar (PBM^1); diastema length (DL); postpalatal length (PPL; from the posterior edge of palate to anterior edge of foramen magnum); lingual palatal breadth at the upper third molar (LBM^3); braincase height (BH; taken at the midline); breadth of M^1 (BM1); breadth of upper incisors (BIT; near tip but below the wear surface); and width of the zygomatic plate (ZP; at its midpoint).

We used Microsoft Excel for Windows (version 2007) to calculate descriptive statistics (mean, standard deviation, and observed range) for sample groups. We assessed quantitative phenetic variation in craniodental morphology through PCA with the use of the correlation matrix of log-transformed measurements of adult specimens using SYSTAT 10 for Windows (SPSS Inc., 2000). Samples included adults of both sexes, usually 10–12 individuals per sex per locality or species, as shown in the tables. Samples were smaller only when more adult individuals were not available. We conducted analyses that included several combinations of taxa, such as all species, sets of closely related species, and geographic populations within species, as described below. We considered any component with an eigenvalue of less than 1.5 to be not meaningfully interpretable and have dealt cautiously with eigenvalues between 2.0 and 1.5, as indicated in the text.

DNA Sequencing and Phylogenetic Analyses

We extracted DNA from and sequenced the entire cytochrome (cyt) *b* gene for 107 individuals of *Apomys*. Sequences have been submitted to GenBank under accession numbers HM370984–HM371090; accession numbers for all analyzed individuals are listed in Appendix 1. The alignment and trees have been deposited with TreeBASE accession S10997. Our use of informal species designations for undescribed species in the small-bodied group (e.g., "sp. F") follows Heaney et al. (1998) and Steppan et al. (2003), except that their "sp. D" has been described as *A. camiguinensis* by Heaney and Tabaranza (2006).

We extracted total genomic DNA from liver or muscle tissue stored in ethanol according to standard phenol/chloroform extraction techniques. We amplified the entire cyt *b* gene by polymerase chain reaction (PCR) following procedures described in Steppan et al. (2003). All PCR reactions included a negative control (no template DNA), intended to identify any instances of contamination of reagents, and were visualized on agarose gels with ethidium bromide. Successful reactions were prepared directly by enzymatic digestion with Exo-SAP-IT (USB Corp., USA). Both strands of each PCR product were completely sequenced with PCR and internal primers. Products were sequenced by automated DNA sequencing on an ABI 3100 with the use of big-dye terminator chemistry (Applied Biosystems, USA). Sequences were aligned by Sequencher 4.1 (Genecodes).

To verify the taxonomy of individuals attributed to *A. datae* and *A. abrae*, we also sequenced individuals collected from the type localities. For specimens from the 1940s and 1950s, we conducted extractions on bits of dried tissue left adhering to museum skulls (FMNH 62709, 62724, 62749, 92759, 92760), the sequencing products of which are referred to as "ancient DNA." Standard procedures were modified by the addition of 10 µl *N*-phenacylthiazolium bromide (PTB) solution to the 200 µl of extraction buffer to break DNA–protein cross-linking (Poinar et al., 2003), incubating for 36 hours rather than overnight. All extractions were conducted in an isolated lab free of PCR products, and ancient DNA PCR and cloning were conducted in a lab that had never worked on mammalian DNA. We amplified a portion of cyt *b* in two overlapping fragments of approximately 110 base pairs in length each, with the use of primer pairs S205/S206 (CCCCCTCCAAYATTT-CATCCTGATGAAA/GTKACTGAGGAGAAGGCAGT) and S207/S208 (TCTAGCCATACACTATACATCAG/CGTCCTACGTGTAGAAATAAGCAG), modified from primers L14841/H14927 and L14925/H15052, respectively, from Kuch et al. (2002), tailored to match *Apomys*. PCR products were then cloned with the TOPO TA cloning kit from Invitrogen and vector pCR 2.1-TOPO (3.9 kb). The recombinant plasmids were isolated with Qiaprep spin columns from Qiagen. Presence of insert and the size of the insert were verified by *Eco*R1 restriction digest and gel electrophoresis. Three to five clones of each ancient sample were sequenced using the vector primers m13r and m13f.

Phylogenetic analyses were conducted using maximum-likelihood (ML) and Bayesian approaches as implemented in PAUP* 4.0b10 (Swofford, 2002) and MrBayes ver. 3.1.2 (Huelsenbeck & Ronquist, 2003). Support values are reported below for ML analyses as bootstrap values (bp) and for Baysian analyses as posterior probabilities (pp). The analytical model (GTR with invariant sites and gamma distributed rates) was identified using Akaike's Information Criterion as implemented in Modeltest 3.04 (Posada & Crandall, 1998) on one of the maximum parsimony (MP) trees. We then conducted a ML search using the preferred model with parameters fixed at the values estimated on the MP tree. A heuristic search was conducted with ten random-addition replicates and TBR branch swapping. Bayesian analysis was run with two heated chains and default settings for 10 million generations each. The data were partitioned by codon, and all parameter values were estimated for each partition separately (unlinked). Convergence was estimated by means of diagnostics from AWTY (Wilgenbusch et al., 2004) as well as by examination of likelihood plots and posterior probabilities of individual clades for subsets of the runs. Trees were recorded every 2000 generations and the first 20% were discarded as burn-in. Nonparametric ML bootstrapping (Felsenstein, 1985) was performed with 200 replicates, each consisting of five random-sequence addition replicates, each of which was limited to 2000 rearrangements.

Karyology

Karyotype preparations were made in the field from freshly caught specimens of some taxa. For live-trapped animals, bone marrow cells were processed with the use of in vivo methods (Patton, 1967, as modified by Rickart et al., 1989). For specimens captured in snap traps and recovered shortly after death, cells were processed with a modified in vitro technique (Rickart et al., 1998). Fixed cell preparations were stored at −70°C within one month of field processing, and standard karyotypes (undifferentially stained with giemsa) were prepared after several months of storage. A minimum of 10 chromosome spreads was examined from each preparation. Chromosome terminology follows Rickart and Musser (1993). As used here, fundamental number (FN) refers to the total number of chromosome arms (including those of sex chromosomes) in the female karyotype. Because of variation in preparation quality and the presence of very tiny secondary arms on some chromosomes, we use the symbol "≥" to indicate what we consider to be minimum FN values.

Results

The Definition of *Apomys*

Apomys is defined as including the most recent common ancestor of *A. datae*, *A. gracilirostris*, *A. hylocoetes*, *A. musculus*, and all its descendants. They are medium to small mice, with adults weighing from as little as 18 g (*Apomys musculus*; Heaney et al., 1999) to as much as 128 g. The general appearance (Figs. 1, 2) resembles individuals of *Peromyscus*, *Apodemus*, *Praomys*, and many other muroid genera. The tail is nearly equal in length to, or longer than, the head and body and usually is dark dorsally and pale to white ventrally, usually with a sharp boundary. The eyes and ears are large. The fur is soft and thick, darker dorsally than ventrally; the ventral fur is paler, often nearly white with an ochraceous wash. The hind feet are moderately long and narrow, have six plantar pads, and have digits 2–4 notably longer than digit 5 and the hallux. All species have two pairs of inguinal mammae.

The skull (Fig. 4) is similar in general appearance to those of many murids of similar size, but a combination of eight characters uniquely diagnoses the genus (Musser, 1982; Musser & Heaney, 1992). 1) The rostrum is moderately to distinctly long and narrow. The premaxillaries project well beyond the anterior edges of the incisors; together, with the equally elongate nasals, this forms a somewhat tubular structure. 2) The incisive foramina are rather broad, especially relative to their length. 3) The bony palate is wide and long, ending posterior to the last molar, with a ridge along the posterior margin. It is textured by many tiny pits and perforations, particularly on the posterior half to one-third of its length. 4) Each upper third molar is small and peg-like, but with a small cusp at the anterolabial margin (absent on worn teeth). 5) The occlusal surface of each first and second upper molar consists of three chevron-shaped laminae on which cusps are barely evident or absent. 6) The occlusal surface of each first lower molar consists of a large, inverted, heart-shaped structure at the front that forms about half of the tooth, followed by a chevron-shaped lamina and a small posterior cingulum. 7) Each auditory bulla is separated from the squamosal and alisphenoid by a gap of variable size; the gap represents the coalesced postglenoid foramen, the postalar fissure, and the middle lacerate foramen. 8) Most species have a subsquamosal fenestra (= squamoso-mastoid fenestra) that is evident as a notch dorsal to the auditory bulla. Additionally, we note that adult male *Apomys* have the posterior tip of the scrotum (roughly 10% of the scrotum) eovered with a densely pigmented, dark spot. A similar pigmented area occurs in *Chrotomys* and *Rhynchomys*.

Apomys is the basal member of a clade that also includes *Archboldomys*, *Chrotomys*, and *Rhynchomys* (Jansa et al., 2006; Heaney et al., 2009). Although no gene sequence data are available from some Indo-Australian genera of interest, this Philippine clade is well supported by multiple nuclear and mitochondrial genes as most closely related to the remaining members of the Hydromyini *sensu* Rowe et al. (2008), all of which are confined to New Guinea, Australia, and adjacent islands (Rowe et al., 2008). *Chiropodomys*, a genus confined to continental SE Asia, the Sunda Shelf, and Palawan, is the sister-group to the Hydromyini *sensu* Rowe et al. (2008; see also Heaney et al., 2009).

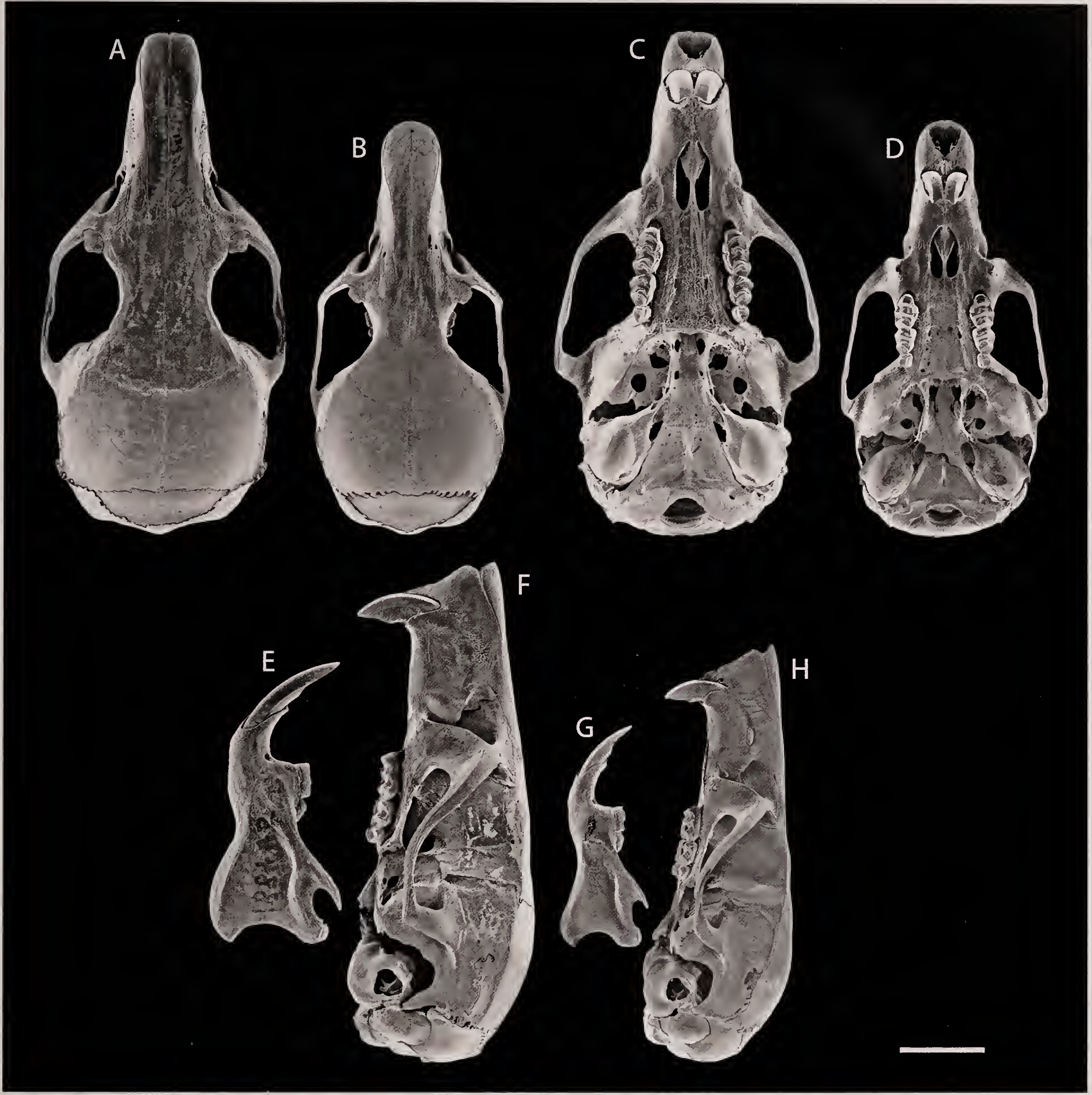


FIG. 4. Crania and mandibles of *Apomys* (*Megapomys*) *datae* (**A**, **C**, **E**, **F**; FMNH 188445) and *Apomys* (*Apomys*) *hylocoetes* (**B**, **D**, **G**, **H**; FMNH 148146), dorsal (**A**, **B**), ventral (**C**, **D**), lateral (**E–H**); scale bar = 5 mm.

Carotid Circulatory Patterns

As noted by Musser (1982), the basicranial arterial circulatory patterns in *A. abrae* and *A. datae* have discrete and fundamental differences; we follow him in referring to these as the "abrae pattern" (Fig. 5A) and "datae pattern" (Fig. 5B). In *A. datae* (Fig. 5B), the carotid artery produces a branch, the stapedial artery, near the posterior margin of the bulla. The carotid artery continues anteriorly through the carotid canal into the cranial cavity where it passes beneath the brain. The stapedial artery enters the bulla through a canal that leads to the stapedial foramen, which lies between the bullar capsule and the petrosal portion of the petromastoid bone. This stapedial foramen is visible on the bulla of a clean skull under low magnification and is visible to the naked eye of many people. The artery proceeds through the bulla and emerges in the middle lacerate foramen as the internal maxillary artery, which courses through a groove in the pterygoid plate and through the foramen ovale into the alisphenoid canal and sphenoidal fissure and eventually into the orbit. This configuration of the carotid circulatory pattern is widespread in murids, and it is present in *Archboldomys*, *Chrotomys*, and *Rhynchomys*, which form the sister-group to *Apomys* (Balete et al., 2006, 2007; Jansa et al., 2006); we

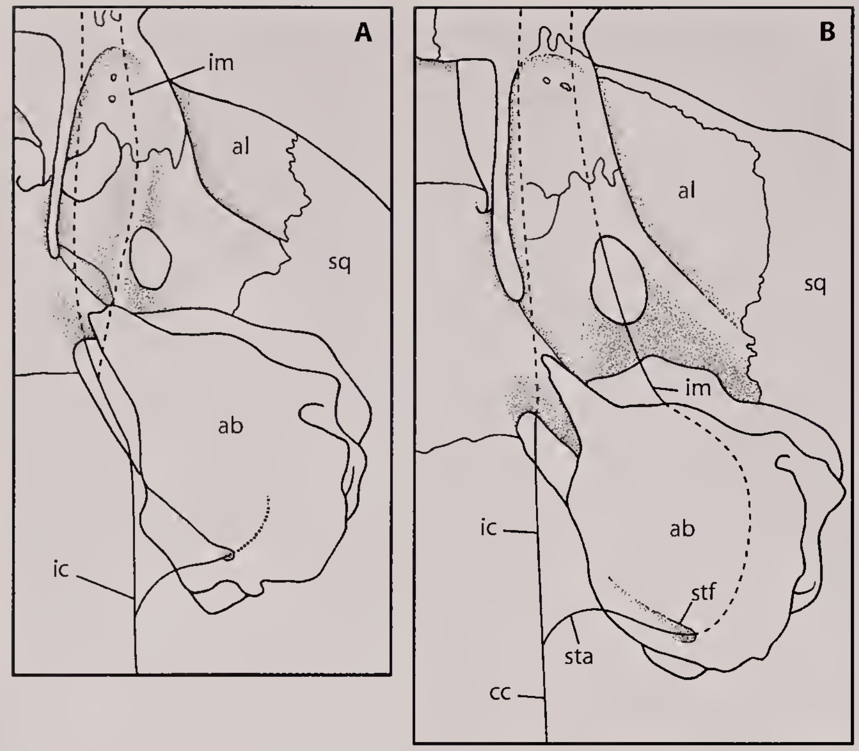


FIG. 5. Diagrammatic drawing of the basicranial region of *Apomys* in ventral view, showing the two types of carotid circulatory patterns. (**A**) The "abrae type"; (**B**) the "datae type." Redrawn from Musser, 1982. Abbreviations: **ab**, auditory bulla; **al**, alisphenoid bone; **cc**, carotid canal; **ic**, internal carotid artery; **im**, internal maxillary artery; **sq**, squamosal bone; **sta**, stapedial artery; **stf**, stapedial foramen.

presume it to be the primitive condition in *Apomys*. It is present in *A. datae*, *A. aurorae* sp. nov., *A. gracilirostris*, *A. magnus* sp. nov., *A. minganensis* sp. nov., and *A. zambalensis* sp. nov., as detailed below.

In *A. abrae* (Fig. 5A), the carotid artery produces a stapedial artery that enters the bulla through a foramen that is too small to be seen with the naked eye and is seen only with difficulty under low magnification. This artery ends within the otic region of the bulla. The carotid artery proceeds anteriorly through the carotid canal into the cranial cavity; at the point of entering the cranial cavity, it produces the internal maxillary artery. The internal maxillary proceeds through a conspicuous groove in the alisphenoid wing of the pterygoid plate, thence through the sphenoidal fissure into the orbit. This condition is present in *A. abrae*, *A. banahao* sp. nov., *A. brownorum* sp. nov., *A. sacobianus*, and *A. sierrae* sp. nov.; we have noted no variation within any of these species. Because this condition is unusual within murids and absent in the sister-clade to *Apomys*, we consider it to be derived within *Apomys*.

On the basis of our assessment of polarity, the molecular phylogeny presented below implies that the primitive "datae pattern" is retained in *A. gracilirostris* (the basal species in the clade), *A. datae*, and the clade that includes *A. minganensis* sp. nov., *A. magnus* sp. nov., *A. aurorae* sp. nov., and *A. zambalensis* sp. nov. The derived condition (the "abrae pattern") developed independently three times: in *A. brownorum* sp. nov. and *A. banahao* sp. nov., in *A. abrae*, and in *A. sierrae* sp. nov. Because the phylogenetic position of *A. sacobianus* is unknown, we do not know whether its possession of the derived condition is shared with one of the other species or is also derived independently. The basicranial arterial patterns are highly useful as diagnostic features of species in *Apomys*, but apparently they are not consistent indicators of phylogenetic relationships as inferred from cyt *b* sequence data analysis.

TABLE 1. Character loadings, eigenvalues, and percent variance explained on the first four components of a principal components analysis of log-transformed measurements of adult large-bodied *Apomys* (see Fig. 6 and Methods).

Variable	Principal component			
	1	2	3	4
Basioccipital length	0.924	0.131	−0.210	0.023
Zygomatic breadth	0.843	0.125	0.147	−0.097
Rostral depth	0.839	−0.028	−0.094	−0.221
Labial palatal breadth at M^1	0.789	−0.485	0.070	0.122
Mastoid breadth	0.766	0.211	0.232	0.002
Orbitotemporal length	0.762	−0.300	−0.120	−0.216
Maxillary toothrow length	0.715	−0.525	0.037	−0.075
Lingual palatal breadth at M^3	0.711	−0.319	−0.237	0.072
Nasal length	0.690	0.405	0.109	0.275
Interorbital breadth	0.650	0.082	0.276	0.285
Diastema length	0.644	0.320	−0.462	0.216
Postpalatal length	0.625	0.272	−0.394	−0.320
Breadth of incisors at tip	0.621	0.105	0.123	−0.507
Width of zygomatic plate	0.618	−0.184	0.049	0.279
Rostral length	0.600	0.616	0.059	0.270
Incisive foramen length	0.541	−0.306	−0.372	0.133
Breadth of M^1	0.488	−0.401	0.584	0.112
Braincase height	0.479	0.374	0.448	−0.302
Eigenvalue	8.665	1.947	1.363	0.965
Percent variance explained	48.14	10.82	7.57	5.36

Quantitative Morphometric Variation within Large-Bodied *Apomys*

We conducted a PCA of 18 craniodental measurements of individuals representing all of the genetic units identified below on the basis of data summarized in the tables of measurements that appear below. Because the genetic data showed that animals from high elevations are often distinct from those at low elevations in a given area, we measured specimens along as complete a portion of the elevational gradient as possible in every case. We included individuals from every geographic region from which we have specimens with complete skulls, to determine whether the operational units apparent in the craniodental morphometric data are evident as monophyletic groups in the genetic data also. In this analysis, we excluded the Mindoro species *A. gracilirostris*. Compared with the other species, it is morphologically divergent, possessing an elongate rostrum, globose braincase, and narrow incisors, conformations not seen in any of the Luzon species. Including this distinctive species with the others, which resemble each other more closely, would have dominated the pattern of variation and obscured fine discrimination among the remaining taxa.

The PCA produced four axes with eigenvalues that exceed or nearly equal 1.0 (Table 1), which explained 48.1%, 10.8%, 7.6%, and 5.4% of the variance in the data set (71.9% total). Loadings on the first axis are all positive and fairly high, indicating that this is an axis that primarily shows overall size. The second axis has strong positive loadings for nasal, rostral, and diastema length and braincase height, and strong negative loadings for the length of the maxillary toothrow, labial breadth of the palate at M^1, lingual palatal breadth at M^3, and breadth of M^1. This axis thus contrasts individuals with long rostra, nasal bones, and diastema, high braincase, short molar toothrows, narrow palates, and narrow M^1, with individuals having the converse.

The third axis (Table 1), with a marginally interpretable eigenvalue of 1.4, had high positive loadings for breadth of M^1

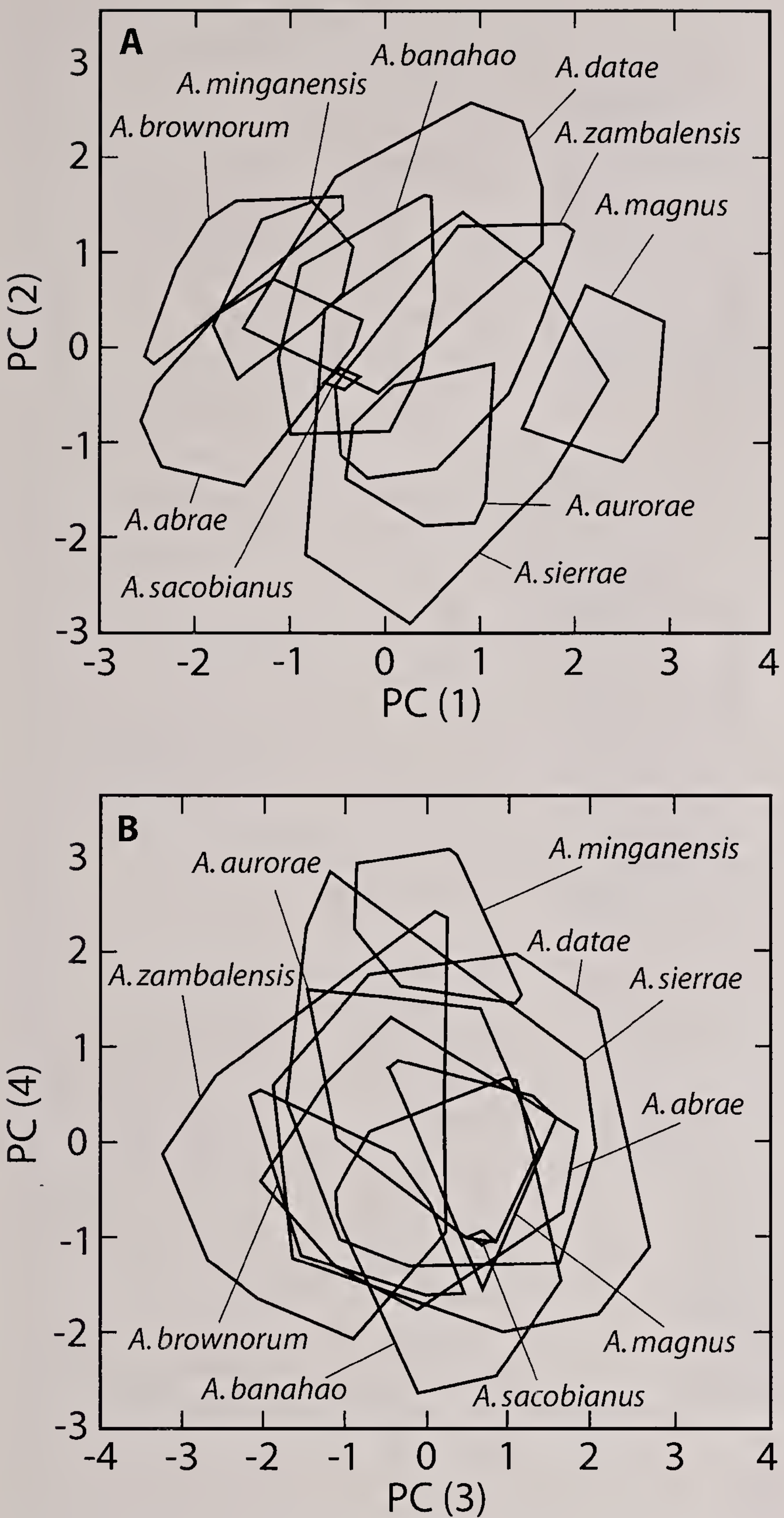


FIG. 6. Results of the principal components analysis of all taxa; see Table 1 and text for details. (**A**) Principal component (PC) 2 vs. PC 1; (**B**) PC 4 vs. PC 3.

and braincase height and high negative loadings for diastema length, length of the incisive foramina, and postpalatal length. This axis contrasts individuals with wide M^1; high braincases; and short diastemas, incisive foramina, and postpalatal regions with those that have the converse.

The fourth axis is not interpretable, with an eigenvalue of 0.965. It primarily contrasts individuals with upper incisors that are narrow at the tip with those that are wider at the tip.

A plot of the first two axes (Fig. 6A) shows overlap among many named species and previously unnamed, geographically defined populations, but clear patterns and differences are nevertheless evident. Specimens from the lowlands of Mt. Banahaw (*A. magnus* sp. nov.) scored highest on the first axis, and specimens of *A. abrae* and those from the high elevations on the Zambales Mountains (*A. brownorum* sp. nov.) scored lowest, reflecting their status as the largest and smallest of these species. Other species fell toward the middle of the range and overlapped extensively. *Apomys datae* scored highest on the second axis, reflecting its long rostral region (including the diastema), high braincase, narrow M^1, and narrow palate (and, we note from examination of skulls, the palate is also short). Most individuals from the Sierra Madre (*A. sierrae* sp. nov.) scored low on this axis, reflecting their shorter rostrum, low braincase, and wide M^1.

Close inspection of Figure 6A shows additional patterns. *Apomys abrae* and *A. datae*, which co-occur in the Central Cordillera, show limited overlap on these two axes. Specimens from high (*A. brownorum* sp. nov.) and low (*A. zambalensis* sp. nov.) in the Zambales Mountains show no overlap; the same is true for specimens from high (*A. banahao* sp. nov.) and low (*A. magnus* sp. nov.) on Mt. Banahaw, and from high (*A. minganensis* sp. nov.) and low (*A. aurorae* sp. nov.) in the Mingan Mountains. Those from high in the Zambales (*A. brownorum* sp. nov.) and on Mt. Banahaw (*A. banahao* sp. nov.) do not overlap, nor do those from low in Zambales (*A. zambalensis* sp. nov.) and on Mt. Banahaw (*A. magnus* sp. nov.). This suggests that each of these is a distinct morphotype, compared with a sympatric or parapatric morphotype. But this analysis also leaves ambiguity among some geographic populations. Individuals from the Sierra Madre and Caraballos Mountains (described below as *A. sierrae* sp. nov.) vary widely, and overlap broadly with individuals from the Mingan lowlands and Zambales lowlands. *Apomys datae* overlaps fairly extensively with individuals from the high elevations on Mt. Banahaw (*A. banahao* sp. nov.) and the Zambales lowlands (*A. zambalensis* sp. nov.), and there is some overlap between *A. datae* and individuals from the Sierra Madre and Caraballos Mountains (*A. sierrae* sp. nov.).

Figure 6B, which is marginally interpretable because of low eigenvalues, plots the scores of individual specimens on axes 3 and 4 of the PCA. *Apomys* from the lowlands of Zambales (*A. zambalensis* sp. nov.), which fall near the center in Figure 6A, score lowest on axis 3, indicating that they have narrow M^1, low braincases, and long diastemas and incisive foramina. *Apomys datae* and specimens from the highlands of Mt. Banahaw (*A. banahao* sp. nov.) have the reverse. On axis 4, specimens from the Mingan highlands (*A. minganensis* sp. nov.) score high, indicating that their incisors are especially narrow at the tip. Specimens from the highlands of Mt. Banahaw (*A. banahao* sp. nov.) scored especially low on this axis. Specimens of *A. sierrae* are notably variable on this axis.

These morphometric analyses provide an overview of differences in size and shape among geographic populations of large-bodied *Apomys*, and many of these differences imply that many distinct species are present. However, clear resolution of species requires further data, which we provide next in the form of genetic data from the mitochondrial DNA genome, specifically from cyt *b*, followed by detailed comparisons of external and craniodental morphology. In the descriptions of species that follow, we also present PCAs of selected sets of species, and of populations in geographically widespread species, as a means of further investigating patterns of variation, similarity, and dissimilarity.

Molecular Evidence of Relationships within *Apomys*

Maximum likelihood analysis of the mitochondrial gene cyt *b* yielded 14 trees, all of which agreed on the among-species

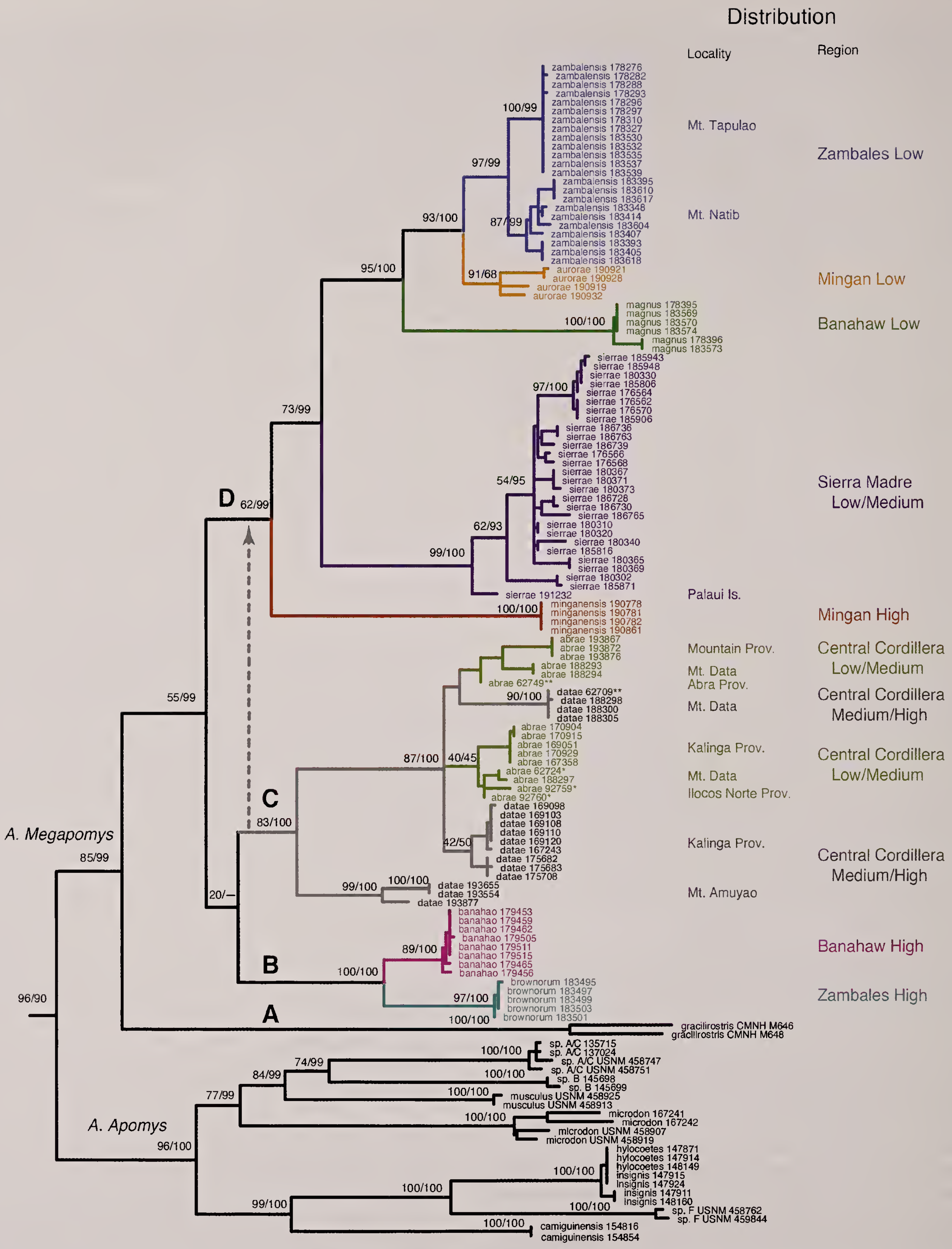


FIG. 7. Maximum likelihood phylogeny of *Apomys* based on the mitochondrial gene cyt *b*. Pictured is one of 14 most likely trees, chosen randomly. The trees vary topologically only with respect to apparent polytomies within species and among three lineages of *A. abrae* and *A. datae*. Support values are ML bootstrap and Bayesian posterior probabilities, respectively, expressed as percentages, for selected nodes. The **long dash symbol** (—) indicates clades B and C are not sister-groups in the maximum credible tree from Bayesian analysis. The **dashed grey arrow** indicates the Bayesian placement of clade C. Unless otherwise specified, all specimen numbers are FMNH. An **asterisk** (*) on the specimen name indicates source for ancient DNA or degraded frozen sample. A **double asterisk** (**) indicates an ancient DNA specimen collected from type locality. Outgroups are pruned for visual clarity. Clades are color-coded by morphologically defined species. Localities and regions of selected clades are indicated on the right. Low, medium, and high refer to relative elevation ranges.

topology. The only differences among the ML trees occurred within regions of near-zero branch lengths: at the base of *A. aurorae*, within *A. sierrae*, and among three population-level clades of *A. datae* and *A. abrae*. Our analysis of the phylogeny showed clear structure, with most nodes significantly resolved down to a low divergence level (Fig. 7). Two primary clades are evident. The first of these (*A. Apomys* in Fig. 7) includes all of the small species (average 18–41 g) in the genus (*A. camiguinensis, A. hylocoetes, A. insignis, A. microdon, A. musculus*, and unnamed taxa labeled "sp. A," "sp. B," "sp. C," and "sp. F"; see Heaney et al., 1998; Steppan et al., 2003). This clade occurs widely within the Philippines except for three areas: the Palawan region, which shares many species with Borneo and may have been connected to Asia (via Borneo) at some point during the Pleistocene glaciations (Heaney, 1985, 1986; Sathiamurthy & Voris, 2006); the small, isolated islands of the Babuyan and Batanes groups that lie north of Luzon; and the Sulu Archipelago, a seemingly depauperate but poorly known set of small islands between Mindanao and Borneo. These species all have tails that are substantially longer than the length of the head and body (from 120% to 140%), and all apparently forage frequently or primarily above ground in grass, shrubs, trees, or a combination thereof, often in sympatry with large-bodied species in northern and central Luzon (Heaney et al., 1989, 1998, 1999, 2006a,b; Rickart et al., 1993, 2011; Balete et al., 2009).

The second primary clade within *Apomys* (*A. Megapomys* in Fig. 7) includes large-bodied animals (mean weight 66–109 g) that occur only on Luzon and Mindoro islands, represented among previously described species by *A. abrae*, *A. datae*, *A. gracilirostris*, and *A. sacobianus* (the last of which could not be included in Fig. 7 because it is known only from the holotype collected in 1956). In addition to these species, which are treated in detail below, many monophyletic lineages are represented by specimens that have been obtained by our field surveys since 2000. All of these mice have tails that are usually about equal to but sometimes shorter than or slightly longer than the length of head and body (84–110%), and they forage on or occasionally slightly above the surface of the ground (Heaney et al., 2003; Duya et al., 2007, this volume; Balete et al., 2009, this volume; Alviola et al., this volume; Rickart et al., 2011).

Within the large-bodied *Apomys*, four secondary clades are evident in the genetic data (Fig. 7). The first of these ("A") consists of *A. gracilirostris* from Mt. Halcon, Mindoro Island, sister to all other species. This is the only large-bodied species of *Apomys* currently known from an island other than Luzon, with the exception of a population on a small, shallow-water island (Palaui) of a species described below that occurs on the adjacent portion of Luzon.

The second large-bodied clade ("B") includes two monophyletic populations from high elevations on Mt. Banahaw and on Mt. Tapulao in the Zambales Mountains (Fig. 3), described herein as the new species *A. banahao* and *A. brownorum*, respectively. Although the genetic distance between them is not great (3.6% uncorrected distance), the support values are high (ML bootstrap 89–97 bp, 1.00 Bayesian pp), and the clade containing these two species is genetically quite distinct from their sister-clade. These populations were easily distinguished from each other on principal components 1 and 2 (PC1, PC2) in the PCA described above and differ in anatomical details described below.

The third large-bodied clade ("C") includes two named species, *A. abrae* and *A. datae*. The results are equivocal as to the exact placement of this clade; ML places it as sister to clade "B," Bayesian analysis places it as sister to clade "D," as discussed below, but neither position is well supported (20% bp, 0.63 pp, respectively). Therefore, we consider the relationships among clades B–D to be unresolved and effectively a polytomy, pending further data. Monophyly of clade C is moderately well supported, with 83% bp and 100 pp. These two species are easily distinguished by morphological details provided below in the species descriptions. The remarkable pattern here is the paraphyly of both species with respect to each other. Individuals assignable morphologically to *A. datae* belong to three mitochondrial lineages, one of which (FMNH 193554, 193655, 193877) is from Mt. Amuyao and is moderately divergent from the rest of the complex. The other two interdigitate with two lineages assignable to *A. abrae*. Specimens from the type localities of these two species are indicated by "**" and are part of this polytomy. Within clade C, cyt *b* data do not support the species limits that are indicated by morphology. There are two leading alternative explanations for this discordance. The species could have diverged only very recently, with the tree reflecting a lack of sorting of the mitochondrial genome. Given that the mitochondrial genome is quickly evolving and rapidly sorting, we believe that this hypothesis is unlikely. Alternatively, mitochondrial introgression might obscure the true phylogeny, as seen in chipmunks (Good et al., 2008). In contrast to the cyt *b* results, preliminary phylogenies from several nuclear genes indicate that these species might not even be close relatives (S. J. Steppan, unpubl. data). We are currently testing these alternatives with additional nuclear sequence data and will present the results elsewhere. Although we consider their current phylogenetic placement tentative pending these further studies, on the basis of their distinctive morphology and extensively overlapping geographic distributions, we retain *A. abrae* and *A. datae* as distinct species.

The fourth major clade ("D" in Fig. 7) includes five distinct monophyletic groups from 1) lowland portions of Mt. Banahaw (described here as *A. magnus* sp. nov.), 2) Mt. Natib and lowland portions of Mt. Tapulao in the Zambales Mountains (described here as *A. zambalensis* sp. nov.), 3) the upper and 4) lower elevations in the Mingan Mountains (described here as *A. minganensis* and *A. aurorae* spp. nov., respectively), and 5) individuals from the northern Sierra Madre, the Caraballo Mountains, and the near-shore, shallow-water island of Palaui (described here as *A. sierrae* sp. nov.). Clade D is the least well supported of the major large-bodied clades, with 62% bp and 0.99 pp.

The first species to diverge in this group is *A. minganensis* sp. nov. from the highlands of the Mingan Mountains. Its genetic distance to other groups is high (7–8% uncorrected, 11–12% ML distances), and support values are strong (100% bp, 1.00 pp), clearly showing this as an evolutionarily distinct species. As described below, this species overlaps syntopically with individuals of *A. aurorae* sp. nov. from the lowlands of the Mingan Mountains, a species that is more closely related to lowland populations from Mt. Banahaw (*A. magnus* sp. nov.) and the Zambales/Natib area (*A. zambalensis* sp. nov.). The absence of evidence of gene flow and the ease of morphological differentiation evident in the PCA (Fig. 6A) mark the two clades in the Mingan Mountains as necessarily representing different species. The clades from lowland

Banahaw (*A. magnus* sp. nov.) and lowland Zambales/Natib (*A. zambalensis* sp. nov.) are genetically similar to each other and the clade from lowland Mingan, but each of these three allopatric clades is well supported, they have limited overlap in the PCA (Fig. 6A), and they can be easily distinguished anatomically from one another. We conclude that each should be recognized as a distinct species.

The "Zambales Low" clade (Fig. 7) is made up of individuals from two sampling regions: Mt. Tapulao in the Zambales Mountains and Mt. Natib in Bataan Province. The two populations form reciprocally monophyletic groups, but the subtending branches are very short. The PCA results and anatomical comparisons of specimens from these areas (described below) show no clear evidence of differences, and we note that these two mountains are at nearly opposite ends of a mountain chain that runs 150 km with only a few narrow lowland gaps (Fig. 3). We predict that individuals collected in intervening areas will show evidence of low-level isolation by distance, consistent with recognition of the single species that we describe here as *A. zambalensis* sp. nov.

The remaining clade consists of individuals from a broad portion of the Sierra Madre and Caraballo Mountains in northeastern Luzon, including Cagayan, Quirino, and Nueva Viscaya provinces and the small offshore island of Palaui. They are separated by a long, well-supported branch (99% bp, 1.00 pp) from any other clade. However, within this clade, little if any geographic structure is apparent: individuals from Mt. Cetaceo in Cagayan Province, from the Mungiao Mountains in Quirino Province, and from Mt. Palali in Nueva Viscaya are scattered almost randomly within the clade, and the internal branches are short. The individual from Palaui Island (FMNH 191232) is slightly divergent from the others, which is not surprising for a population on a small island that has been isolated by a shallow sea-channel for about 12,000 years, and periodically during earlier Pleistocene interglacial periods. A PCA of these populations, presented below, showed no evidence of structure within this set of individuals, and we see no evidence of anatomical differences, aside from pelage (see below), among any of these populations, including the one from Palaui Island. It is therefore our hypothesis that all of these individuals are members of a single species, *Apomys sierrae* sp. nov.

We note that two genetically distinct populations occur in the Mingan Mountains: two in the Zambales Mountains and two on Mt. Banahaw. In each of these cases, there is no evidence of hybridization or intermediacy in any individual, and indeed, none of the pairs consists of sister-species. *Apomys abrae* and *A. datae*, on the other hand, which are sympatric over much of the Central Cordillera, currently have ambiguous relationships discussed above and below.

Karyotypic Variation

Karyotype data are available for nine species of *Apomys*, more than half of the 17 species currently known (including the 7 described here). The level of karyotypic variation within *Apomys* is extreme: only two species share a common karyotype (*A. abrae* and *A. datae*), whereas the remaining species have highly divergent karyotypes with diploid numbers ranging from 30 to 48 and fundamental numbers from 50 to 88 (Rickart & Musser, 1993; Rickart & Heaney, 2002). Much of this karyotypic diversity is encompassed among species belonging to the small-bodied clade as defined above.

Among the *Apomys* that have been karyotyped, four belong to the large-bodied clade (Fig. 8). *Apomys datae* (Fig. 8A) and *A. abrae* (Fig. 8B) both have karyotypes of $2n = 44$ that are very similar, if not identical, consisting of a majority of telocentric elements, including a large telocentric X chromosome, and distinctive pairs of biarmed autosomes. *Apomys zambalensis* sp. nov. from Mt. Natib in Bataan Province also has a karyotype of $2n = 44$ (Fig. 8C) but differs in a number of important respects from the *datae–abrae* arrangement, including a submetacentric X chromosome. The karyotype of *A. banahao* sp. nov., from the high elevations on Mt. Banahaw in Quezon Province, has $2n = 48$ (Fig. 8D), but otherwise is most similar to that of *A. zambalensis* sp. nov. Each of these karyotypes of large-bodied *Apomys* is similar to a common karyotype of $2n = 44$ seen in species belonging to the other genera of "earthworm-mice," *Archboldomys, Chrotomys,* and *Rhynchomys* (Rickart & Musser, 1993; Rickart & Heaney, 2002; E. A. Rickart, unpubl. data).

Patterns of karyotype diversity within *Apomys* and related genera suggest that the large-bodied species are more conservative, with arrangements that resemble the presumed ancestral karyotype, whereas members of the small-bodied clade have more highly derived karyotypes. Clearly, diversification within *Apomys* has often been accompanied by major chromosomal evolution.

The Subgenera and Species of Large-Bodied *Apomys*

To recognize the fundamental morphological, genetic, and ecological dichotomy within *Apomys*, we recognize two subgenera within the genus. The subgenus *Apomys* includes the small-bodied species, as listed below, retaining *A. hylocoetes* Mearns 1905 as the type species. For the large-bodied species, we propose the new subgenus *Apomys* (*Megapomys*).

Apomys (*Megapomys*) New Subgenus

TYPE SPECIES—*Mus datae* Meyer, 1899 (= *Apomys datae sensu* Ellerman, 1941, and others).

ETYMOLOGY—From the Greek "megas," meaning large or great; "apo," from Mt. Apo, the highest mountain in the Philippines, and meaning "grandfather" in local languages; and the Greek "mys," meaning mouse. The gender is masculine.

INCLUDED SPECIES—The previously described *A. abrae* (Sanborn, 1952), *A. datae* (Meyer, 1899), *A. gracilirostris* Ruedas, 1995, and *A. sacobianus* Johnson, 1962, and the seven new species described below: *A. aurorae, A. banahao, A. brownorum, A. magnus, A. minganensis, A. sierrae,* and *A. zambalensis.*

DIAGNOSIS—The subgenus *Megapomys* is defined phylogenetically as the most recent common ancestor of *A. gracilirostris*, *A. datae*, and *A. zambalensis* and all of its descendants (Fig. 7), and by the following combination of morphological characters (contrasted with the subgenus *Apomys*): size large, averaging 66–109 g (vs. 18–41 g in *A.* (*Apomys*)); average tail length ranging from 84% to 110% of the length of head and body (vs. 120–140%); hind foot typically relatively broader and wider (vs. longer and narrower; see Heaney & Tabaranza, 2006); braincase more

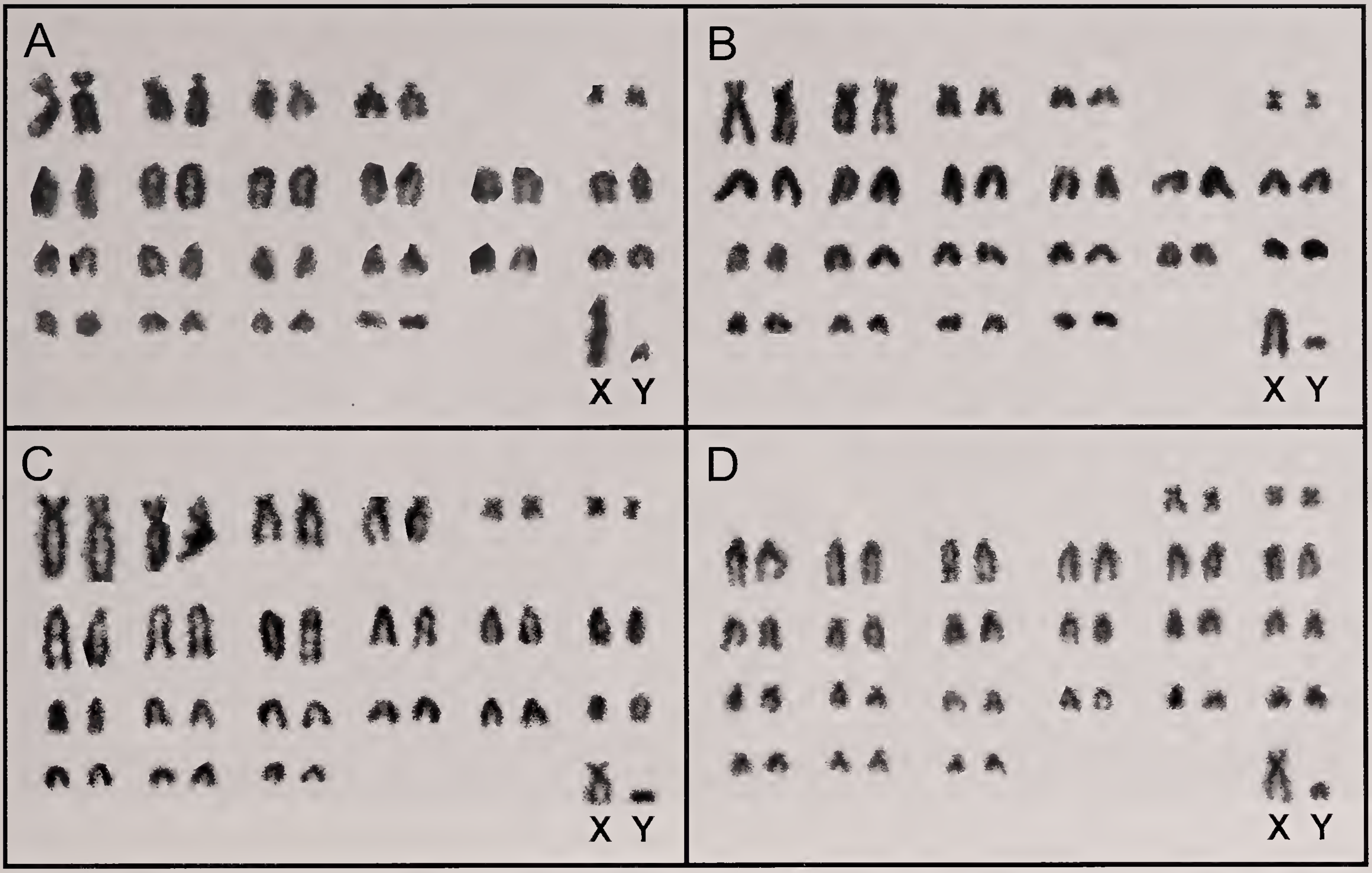


FIG. 8. Male karyotypes of four species of the subgenus *Megapomys* from Luzon. (**A**) *Apomys datae,* Mt. Amuyao, Mountain Province (FMNH 193662). (**B**) *Apomys abrae,* Balbalasang, Kalinga Province (FMNH 169051). (**C**) *Apomys zambalensis* sp. nov., Mt. Natib, Bataan Province (FMNH 183368). (**D**) *Apomys banahao* sp. nov., Mt. Banahaw, Quezon Province (FMNH 178468).

robust, less globose (vs. more delicate and globose; Fig. 4); rostrum proportionately broader and heavier, except in *A.* (*M.*) *gracilirostris* (vs. thinner and more gracile); upper incisors deeper in anteroposterior axis, except in *A.* (*M.*) *gracilirostris* (vs. narrower); posterior bony palate more heavily pitted and fenestrated (vs. less pitted and fenestrated); incisive foramina proportionately broader (vs. broad, but less so); and zygomatic arches more robust (vs. more gracile). Some of these characters are associated with *Megapomys,* being a clade of larger, more ground-living species, compared with the smaller and more arboreal subgenus *Apomys*. These two ecomorphological lineages are clearly evident in the mitochondrial DNA-based analysis (Fig. 7).

The genus *Apomys* has *A. hylocoetes* as its type species, and thus the nominotypical subgenus necessarily does as well. This subgenus contains the following recognized species: *A. camiguinensis*, *A. hylocoetes*, *A. insignis*, *A. littoralis*, *A. microdon*, and *A. musculus,* plus several as yet undescribed species listed by Heaney et al. (1998) on the basis of the cyt *b* phylogenies presented by Steppan et al. (2003) and in Figure 7. These species are widespread in the Philippines, with the exception of the Palawan and Babuyan/Batanes groups of islands and the Sulu Archipelago. On Luzon, *A. microdon* and *A. musculus* often occur sympatrically with members of the subgenus *Megapomys* (e.g., Heaney et al., 1998; Balete et al., 2009; Rickart et al., 2011).

Because the morphometrically distinctive populations of *Megapomys* are concordant with mitochondrial clades (except *A. abrae* and *A. datae*, as discussed) and with units defined on the basis of qualitative external and craniodental traits (as discussed below), we recognize each of them as a distinct species in the following pages. In the diagnoses and comparisons that follow, we emphasize differences that separate species from their sister-taxa and from the geographically closest species of *Megapomys*.

Apomys datae (Meyer, 1899)

Mus datae Meyer, 1899: 52.

Apomys major Miller, 1910: 402. Musser 1982: 73, synonym of *A. datae*.

Apomys datae. Ellerman, 1941: 225. First use of current name combination.

HOLOTYPE—Staatliches Museum für Tierkunde, Dresden B3100 obtained in 1892 by John Whitehead. Prepared as stuffed skin plus skull.

TYPE LOCALITY—"Monte Data, Lepanto [Province], North Luzon, Philippines" (= Mt. Data, currently in Mountain Province; see Musser, 1982).

SPECIMENS EXAMINED (n = 882)—**LUZON ISLAND**: Benguet Prov.: Haight's-in-the-Oaks, 7000 ft [ca. 2100 m] (USNM 151513); Mt. Pulag National Park, 0.5 km S, 0.4 km W Mt. Babadak peak, 2480 m (FMNH 198620–198632, 198638, 198639, 198643–198653, 198662–198665, 198669–198672, 198827, 198828, 198831–198833, 198835–198840); Mt. Pulag National Park, 0.7 km S, 0.4 km W Mt. Babadak peak, 2445 m (FMNH 198536, 198583–198604, 198611–198615); Mt. Pulag National Park, 0.8 km S, 0.4 km W Mt. Babadak peak, 2420 m (FMNH 198579–198582, 198640, 198641, 198654, 198673, 198811–198819, 198834); Mt. Pulag National Park, 0.8 km S, 0.9 km

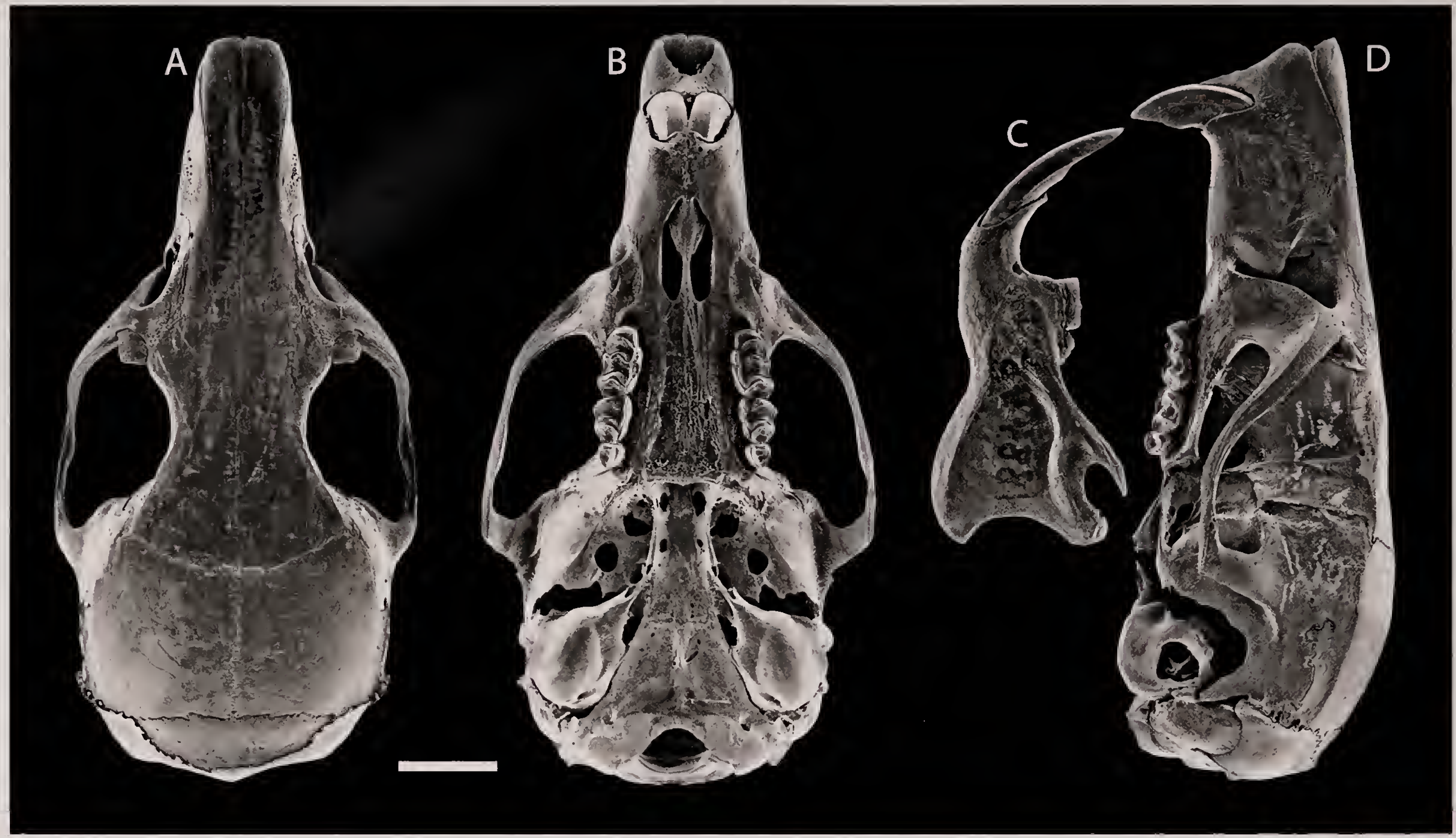


FIG. 9. Dorsal (**A**), ventral (**B**), and lateral (**D**) views of the cranium and lateral view of the mandible (**C**) of *Apomys datae* (FMNH 188445; adult female from Mt. Data); scale bar = 5 mm.

W Mt. Babadak peak, 2285 m (FMNH 198616, 198617, 198633–198637, 198642, 198655–198659, 198667, 198668, 198674–198676, 198825, 198826, 198830); Mt. Pulag National Park, 0.9 km S, 0.9 km W Mt. Babadak peak, 2335 m (FMNH 198605–198610, 198618, 198619, 198660, 198661, 198666, 198677, 198820–198824, 198829); Mt. Pulag National Park, 0.5 km S, 0.7 km E Mt. Pulag peak, 2800 m (FMNH 198539–198543, 198549, 198798, 198801); Mt. Pulag National Park, 0.6 km S, 0.65 km E Mt. Pulag peak, 2730 m (FMNH 198550–198555, 198565–198568, 198570, 198571, 198804–198807); Mt. Pulag National Park, 1.15 km S, 1.35 km E Mt. Pulag peak, 2695 m (FMNH 198556–198564, 198572–198578, 198802, 198803, 198808–198810, 202538); Mt. Pulag National Park, 1.2 km S, 1.15 km E Mt. Pulag peak, 2780 m (FMNH 198544, 198545, 198548, 198799, 198800); Mt. Pulag National Park, 1.35 km S, 0.8 km E Mt. Pulag peak, 2740 m (FMNH 198537, 198538, 198546, 198547, 198569); Mt. Pulag National Park, 1.75 km S, 0.9 km E Mt. Pulag peak, 2650 m (FMNH 198678–198707, 198841–198852).

Ifugao Prov.: Kiangan Munic.: Brgy. Duwit (=Brgy. Duit), 4000 ft [ca. 1200 m] (USNM 557717). Ilocos Norte Prov.: Tagudin (AMNH 252474–252475).

Kalinga Prov.: Balbalan Munic.: Balbalasang Brgy.: Am-licao, 1800 m (FMNH 169071–169121, 170931–170964, 170982); Balbalan Munic.: Balbalasang Brgy.: Magdallao, 1600 m (FMNH 167243, 167244, 167246–167253, 167255–167257, 167260, 167263–167272, 167278–167284, 167288–167291, 167293, 167295–167298, 167302, 167329–167341, 167345, 167348, 167350–167354, 167357, 167359, 167360, 167362–167366); Balbalasang Brgy.: Mt. Bali-it, 1950 m (FMNH 175415–175498, 175630–175681, 175732); Balbalan Munic.: Balbalasang Brgy.: Mt. Bali-it, 2150 m (FMNH 175499–175546, 175682–175717, 175733).

Mountain Prov. (no specific locality; FMNH 62761, 62762); 0.6 km N Barlig Munic. Hall, 1800 m (FMNH 193548, 193549, 193877); 0.4 km N, 0.4 km W Mt. Amuyao peak, 2480 m (FMNH 193599–193614, 193884–193886); 0.5 km N, 0.5 km W Mt. Amuyao peak, 2530 m (FMNH 193550–193559, 193878–193883); 0.75 km W Mt. Amuyao peak, 2300 m (FMNH 193615–193636, 193910–193919); 1.0 km N, 1.0 km W Mt. Amuyao peak, 2150 m (FMNH 193637–193659, 193920–193931); 1.25 km N, 0.5 km W Mt. Amuyao peak, 1990 m (FMNH 193660–193662); 1.75 km N, 0.4 km W Mt. Amuyao peak, 1885 m (FMNH 193932–193940, 193663–193675); 1.75 km N, 1.5 km W Mt. Amuyao peak, 1950 m (FMNH 193676–193680); Mt. Amuyao peak, 2690 m (FMNH 193560–193598, 193887–193909); Mt. Data (FMNH 62697, 62698, 62701–62705, 62707, 62708, 62710, 62713–62718, 62721, 62722, 62729, 62730, 62732, 62735–62737, 62742, 62745–62747); Mt. Data, 5300 ft [ca. 1600 m] (FMNH 62731); Mt. Data, 7500 ft [ca. 2300 m] (FMNH 62695–62696, 62699, 62720, 62725); Mt. Data, 8000 ft [ca. 2400 m] (FMNH 62727, 62733–62734, 62741, 62744); Mt. Data, 8200 ft [ca. 2500 m] (FMNH 62706, 62709, 62711); Mt. Data, 8300 ft [ca. 2500 m] (FMNH 62712); Mt. Data, Cotcot (FMNH 62743, 62748); 0.1 km E south peak Mt. Data, 2310 m (FMNH 188298–188306, 188310–188312, 188438–188445); 0.75 km N, 0.6 km E south peak Mt. Data, 2241 m (FMNH 188245–188277, 188425–188427, 188429–188436, 188493); 0.75 km N, 0.75 km E south peak Mt. Data, 2289 m (FMNH 188287–188291, 188448); 0.75 km N, 1.0 km E south peak Mt. Data, 2289 m (FMNH 188278–188286, 188307–188309, 188446, 188447).

EMENDED DIAGNOSIS AND DESCRIPTION—A large mouse (HBL averaging 137–144 mm, BOL averaging 34–36 mm in populations summarized in Table 2), with a tail that averages shorter than the length of head and body (89–95%; Table 2; Figs. 1B, 9). The fur is dense, soft, and dark brown with a slight rusty-orange tint dorsally. The ventral fur is either white at the tips, or with a pale ochraceous wash, and dark gray at the base. The fur on the dorsal surface of the forepaws and hind feet is white on the distal half, with dark fur extending over approximately the basal half. The tail is darker dorsally than ventrally, often with a sharp line demarcating the upper and lower halves, but some scattered black hairs are often present on the ventral surface of the tail. The skin of the lips and lower rhinarium is darkly pigmented, as is the inside surface of the base of the pinna. The hind feet are of moderate length, with fairly large and well-separated pads, and usually are darkly pigmented over the proximal half to two-thirds of the ventral surface. The plantar pads are large, and the toes are slightly short and stocky (Fig. 10B). The cranium is relatively large and robust, with a deep, squarish braincase and a long, stout rostrum that is associated with a long diastema. The interparietal bone is of variable shape, but usually moderately wide (anteroposteriorly) and roughly oval in shape. The maxillary toothrow is moderately short, the palate is narrow, and the toothrows diverge slightly posteriorly (Fig. 9B; Table 2). The postpalatal region is of moderate length. The stapedial artery enters each bulla through a distinct foramen between the bullar capsule and the petrosal portion of the petromastoid bone (the "datae pattern"; Fig. 5B). The mandible is robust and deep. The coronoid process is slender, sharply pointed, and moderately long; the angular process is sturdy, with the posterior margin of the mandible sweeping down in a shallow arc from the condylar process (Fig. 9C).

On the basis of two males from Mt. Amuyao, Mountain Province (FMNH 193558, 193662), and one from Mt. Bali-it, Kalinga Province (FMNH 169111), the karyotype of *A. datae* has $2n = 44$ and $FN \geq 54$ (Fig. 8A). The available preparations are of marginal quality, but the karyotype appears to be very similar to that of *A. abrae* (described below in greater detail).

To assess geographic variation, we conducted a PCA of 18 craniodental measurements in Table 2 from the four populations of *A. datae* from which we have adequate samples: Mt. Pulag (Benguet Province), Mt. Data and Mt. Amuyao (Mountain Province), and Mt. Bali-it and vicinity (Kalinga Province); these represent populations from the southern, central, and northern portions of the species' range. The first principal component (PC1), which accounted for 36% of the variation, had moderate to high positive loadings for all variables, with the exception of length of incisive foramen, which has a loading barely above zero (Table 4); this component appears to represent overall size. The second component (PC2), which accounted for 11% of the variation, had high positive loadings on length of incisive foramen and diastema and labial breadth at M^3 and high negative loadings on length of the molar toothrow, braincase height, and breadth of M^1. The next two components had eigenvalues of 1.2 or less. Individuals from all four areas overlapped extensively on the first two PCs, with no evident geographic pattern (Fig. 11). Given this lack of quantitative craniodental differences, and the consistent qualitative cranial and external morphology, we regard all of the specimens included in Specimens Examined as being examples of a single species.

COMPARISONS—Relative to most other *Megapomys*, the cranium of *A. datae* is large and robust, with a deep, squarish braincase, a long, stout rostrum, and a long diastema. As detailed below, relative to some other species, the maxillary toothrow is short, the palate is narrow, and the postpalatal region is of moderate length (Fig. 9; Table 2). In *A. datae*, the stapedial artery enters each bulla through a distinct foramen between the bullar capsule and the petrosal portion of the petromastoid bone (the "datae pattern"; Fig. 5B), as discussed above under Carotid Circulatory Patterns.

Compared with *A. abrae*, the tail is short relative to the length of head and body, averaging 89–95% (97–101% of HBL in *A. abrae*; Table 2). A plot of weight and relative length of the tail (Fig. 12A) shows overlap, but most individuals are outside of the area of overlap. The dorsal pelage of *A. abrae* (Fig. 1C) typically is a rich, dark brown, whereas that of *A. datae* is equally dark, but has a rusty, slightly orange tinge (Fig. 1B); although, as noted below, some specimens of *A. abrae* are much paler. *Apomys abrae* rarely have any black hairs on the ventral surface of the tail, whereas scattered black hairs are often present on *A. datae*, and the scales are usually pale gray, not white as in *A. abrae*. The fur on the dorsal surface of the forepaws and hind feet of *A. abrae* is white or with very few scattered dark hairs (vs. having dark hairs extending over much of the tops of the feet). The hind feet of *A. abrae* (Fig. 10A) are paler, slightly shorter on average, and proportionately narrower, than those of *A. datae* (Table 2). Additionally, the toes are slightly longer, and the plantar pads are smaller and more widely separated than those of *A. datae* (Fig. 10B).

The cranium of *A. datae* is larger than that of *A. abrae* in nearly every dimension, with little overlap in zygomatic breadth, mastoid breadth, nasal length, rostral depth, rostral length, width of the zygomatic plate, and postpalatal length (Table 2). For example, plots of zygomatic breadth and mastoid breadth (Fig. 12B) and rostral length and rostral depth (Fig. 12C) show very little overlap, and serve to easily distinguish most individuals. The interparietal bone is variable in both species but is usually anteroposteriorly wider in *A. datae* than in *A. abrae*. Relative to *A. datae*, the mandible of *A. abrae* is shorter and less deep, with a shorter coronoid process, less robust angular process, and more concave posterior margin between the condylar and coronoid processes.

A PCA of individuals that we refer to *A. datae* and *A. abrae* using 18 craniodental measurements (Tables 2, 3) showed significant and interpretable variation on two components (Fig. 13; Table 5). The first component loaded heavily on nearly all measurements (Table 5) and accounted for 51% of the total variation; only length of incisive foramen had a low loading. This axis was thus an overall measure of size and robustness. The second component loaded heavily and positively on length of incisive foramen and diastema length and negatively on length of the molar toothrow, palatal breadth at M^1, and breadth of M^1. A plot of these two components (Fig. 13) showed that specimens with qualitative features associated with *A. abrae* scored low on PC1, and *A. datae* scored high; this is consistent with our observation regarding relative size and robustness of these two species, with some overlap that we suspect is associated with age-related variation in size. PC2 had great overlap, such that it does not assist in distinguishing between these species. Taking all of the available data together, it appears that the differences in carotid artery circulatory patterns, pelage coloration, and overall size are the best means to distinguish between these two species.

DISTRIBUTION—*Apomys datae* occurs widely in the high mountains of the Central Cordillera of northern Luzon Island. Verified records are from Benguet, Ifugao, Kalinga, and Mountain provinces, from 1500 to 2800 m in elevation (Figs. 3, 14). This species overlaps broadly with *A. abrae*, but *A. datae* usually occurs in more mature forests, in moister habitats, and at higher elevations, although they occur syntopically in some places (Rickart et al., 2011; Fig. 15). Surveys are needed to determine the distribution of this species in the northernmost Central Cordillera, in Abra, Apayao, and Ilocos Norte provinces, and in the southeastern Central Cordillera where this range abuts with the Caraballo Mountains, which support *A. sierrae* sp. nov.

TABLE 2. Cranial and external measurements (mean ± 1 S.D. and range) of *Apomys datae* and *A. abrae* (part).

	Apomys datae					
	Mt. Data, Mountain Prov.		**Balbalasang, 1900–2150 m, Kalinga Prov.**		**Mt. Amuyao, Mountain Prov.**	
Measurement	**M (n = 10)**	**F (n = 10)**	**M (n = 10)**	**F (n = 10)**	**M (n = 10)**	**F (n = 10)**
Basioccipital length	35.51 ± 0.75 34.14–36.77	34.82 ± 0.62 34.06–35.90	34.75 ± 0.72 33.65–35.82	33.94 ± 0.55 33.24–34.76	35.02 ± 0.92 33.58–36.58	35.07 ± 0.47 34.46–35.64
Interorbital breadth	6.14 ± 0.28 5.60–6.50	6.07 ± 0.36 5.29–6.50	5.79 ± 0.35 5.20–6.58	5.89 ± 0.23 5.42–6.21	6.21 ± 0.26 5.91–6.71	6.21 ± 0.18 5.90–6.52
Zygomatic breadth	18.55 ± 0.40 17.85–18.99	18.60 ± 0.27 18.09–19.15	18.34 ± 0.41 (9) 17.90–18.98	18.19 ± 0.23 (9) 17.87–18.63	18.15 ± 0.39 (9) 17.60–18.84	18.16 ± 0.40 17.64–18.73
Mastoid breadth	14.68 ± 0.36 14.23–15.48	14.53 ± 0.35 13.86–14.94	14.08 ± 0.30 13.53–14.49	13.99 ± 0.31 13.39–14.46	14.34 ± 0.25 13.85–14.66	14.34 ± 0.21 14.11–14.72
Nasal length	15.15 ± 0.50 14.14–15.85	14.61 ± 0.54 13.89–15.42	14.07 ± 0.32 13.61–14.64	13.76 ± 0.24 13.38–14.23	14.66 ± 0.49 14.03–15.52	14.90 ± 0.45 14.42–15.91
Incisive foramen length	4.94 ± 0.27 4.58–5.29	4.77 ± 0.20 4.48–5.13	5.37 ± 0.17 5.14–5.78	5.28 ± 0.38 4.75–5.87	5.15 ± 0.32 4.58–5.57	5.20 ± 0.26 4.86–5.65
Rostral depth	7.73 ± 0.30 7.14–8.21	7.70 ± 0.22 7.43–8.02	7.42 ± 0.24 7.17–7.91	7.38 ± 0.16 7.16–7.66	7.49 ± 0.17 7.26–7.73	7.45 ± 0.17 7.20–7.69
Rostral length	16.43 ± 0.50 15.51–17.02	16.15 ± 0.40 15.71–17.09	15.58 ± 0.32 15.21–16.16	15.14 ± 0.37 14.61–15.89	16.01 ± 0.62 15.16–17.09	15.97 ± 0.21 15.71–16.36
Orbitotemporal length	11.64 ± 0.27 11.21–11.98	11.68 ± 0.39 11.28–12.60	11.69 ± 0.32 11.23–12.30	11.72 ± 0.34 11.07–12.08	11.31 ± 0.37 10.85–11.84	11.57 ± 0.20 11.31–11.91
Maxillary toothrow length	7.06 ± 0.23 6.82–7.53	7.09 ± 0.16 6.89–7.34	6.93 ± 0.23 6.49–7.25	6.78 ± 0.26 6.48–7.26	6.80 ± 0.19 6.53–7.18	6.86 ± 0.18 6.65–7.21
Labial palatal breadth at M^1	7.31 ± 0.21 7.07–7.70	7.37 ± 0.14 7.22–7.70	7.22 ± 0.16 6.92–7.51	7.17 ± 0.26 6.77–7.50	7.34 ± 0.26 6.96–7.81	7.28 ± 0.22 6.91–7.62
Diastema length	9.45 ± 0.33 9.11–10.06	9.22 ± 0.25 8.89–9.71	9.13 ± 0.23 8.76–9.52	9.18 ± 0.23 8.80–9.59	9.38 ± 0.40 8.95–10.21	9.52 ± 0.27 9.10–9.89
Postpalatal length	12.11 ± 0.32 11.72–12.61	11.89 ± 0.38 11.28–12.36	11.81 ± 0.53 11.09–12.60	11.34 ± 0.36 10.87–12.07	11.64 ± 0.19 11.38–12.00	11.83 ± 0.27 11.46–12.29
Lingual palatal breadth at M^3	5.03 ± 0.23 4.57–5.38	5.08 ± 0.28 4.59–5.47	4.95 ± 0.22 4.60–5.30	4.97 ± 0.22 4.66–5.42	5.02 ± 0.15 4.79–5.28	5.13 ± 0.18 4.88–5.44
Braincase height	11.42 ± 0.32 11.00–11.96	11.45 ± 0.34 10.58–11.81	10.92 ± 0.44 10.23–11.58	10.80 ± 0.28 10.28–11.30	10.55 ± 0.40 9.77–11.02	10.81 ± 0.30 10.40–11.22
Breadth of M^1	1.87 ± 0.05 1.81–1.95	1.90 ± 0.06 1.84–2.03	1.82 ± 0.07 1.69–1.92	1.81 ± 0.08 1.70–1.93	1.83 ± 0.07 1.74–2.01	1.83 ± 0.09 1.71–1.95
Breadth of incisors at tip	2.32 ± 0.11 2.13–2.48	2.24 ± 0.09 2.08–2.37	2.26 ± 0.14 2.02–2.43	2.23 ± 0.07 2.12–2.32	2.17 ± 0.10 2.01–2.30	2.21 ± 0.08 2.13–2.40
Width of zygomatic plate	3.55 ± 0.17 3.20–3.74	3.43 ± 0.22 3.12–3.78	3.53 ± 0.14 3.37–3.82	3.55 ± 0.20 3.22–3.88	3.41 ± 0.16 3.12–3.59	3.55 ± 0.26 3.28–3.96
Length of head and body	144.7 ± 6.9 130–154	141.0 ± 6.0 (9) 129–149	139.4 ± 2.9 (8) 134–142	137.8 ± 4.9 (8) 133–149	138.7 ± 7.2 127–151	139.9 ± 5.2 132–147
Total length	279.5 ± 7.6 260–287	273.3 ± 8.0 (9) 257–286	269.4 ± 5.6 (8) 261–277	261.3 ± 6.9 (8) 256–276	268.9 ± 14.3 250–292	271.5 ± 5.3 262–278
Length of tail vertebrae	134.8 ± 4.6 126–141	132.1 ± 3.6 128–139	130.0 ± 3.9 (8) 125–136	123.5 ± 2.8 (8) 121–127	130.2 ± 7.9 121–141	131.6 ± 4.2 128–142
Length of hind foot	37.3 ± 0.9 36–38	36.2 ± 1.5 33–38	35.5 ± 0.7 34–36	34.5 ± 0.7 33–35	37.0 ± 1.1 35–38	35.8 ± 1.3 34–38
Length of ear	21.0 ± 0.7 20–22	20.3 ± 0.9 18–21	21.1 ± 0.7 20–22	20.7 ± 1.1 19–22	20.6 ± 0.5 20–21	20.5 ± 0.7 20–22
Weight (g)	91.6 ± 7.0 78–102	81.8 ± 9.8 (9) 70–97	72.2 ± 4.6 66–79	70.7 ± 5.9 63–82	77.5 ± 6.4 68–88	79.2 ± 10.2 65–90

COMMENTS—Because this species was the best known of the Luzon *Megapomys* for many years, the few scattered specimens from other parts of Luzon were often tentatively, but incorrectly, referred to this species in collections and in some publications (e.g., Danielsen et al., 1994; Heaney et al., 1998). We have examined the holotype of *A. major* Miller 1910, and agree with Musser (1982) that it is not distinguishable from *A. datae* and should be treated as a junior synonym.

Apomys abrae (Sanborn, 1952)

Rattus (*Apomys*) *abrae* Sanborn, 1952: 133.

Apomys abrae. Johnson 1962. First use of current name combination.

HOLOTYPE—FMNH 62750, young adult male, obtained 14 May 1946. Field number H. H. Hoogstraal 460. Prepared as stuffed skin plus skull. Measurements in Table 2.

TYPE LOCALITY—Philippines: Luzon Island: Abra Province: Massisiat, 3500 feet [ca. 1100 m] (approximately 17.583°N, 120.833°E; our estimate from topographic maps). Taken in "thick growth along mountain creek" (from specimen tag).

SPECIMENS EXAMINED (n = 183)—**LUZON ISLAND**: Abra Prov.: Massisiat, 3500 ft [ca. 1100 m] (FMNH 62749; 62750).

Benguet Prov.: Baguio (USNM 151510, 399580); Baguio, 3000 ft [ca. 900 m] (USNM 399573–399577); Baguio, 3600 ft [ca. 1100 m] (USNM 399579); Baguio, 4000 ft [ca. 1200 m] (USNM 399578); Haight's-in-the-Oaks, 7000 ft [ca. 2100 m] (USNM 151507–151509, 151530, 261170); near Baguio (MCZ 35034, 35035); near Baguio, Mt. Santo Tomas (AMNH 242099, 242100; FMNH 202181); Sablan (FMNH 92763, 92764).

TABLE 2. *Extended.*

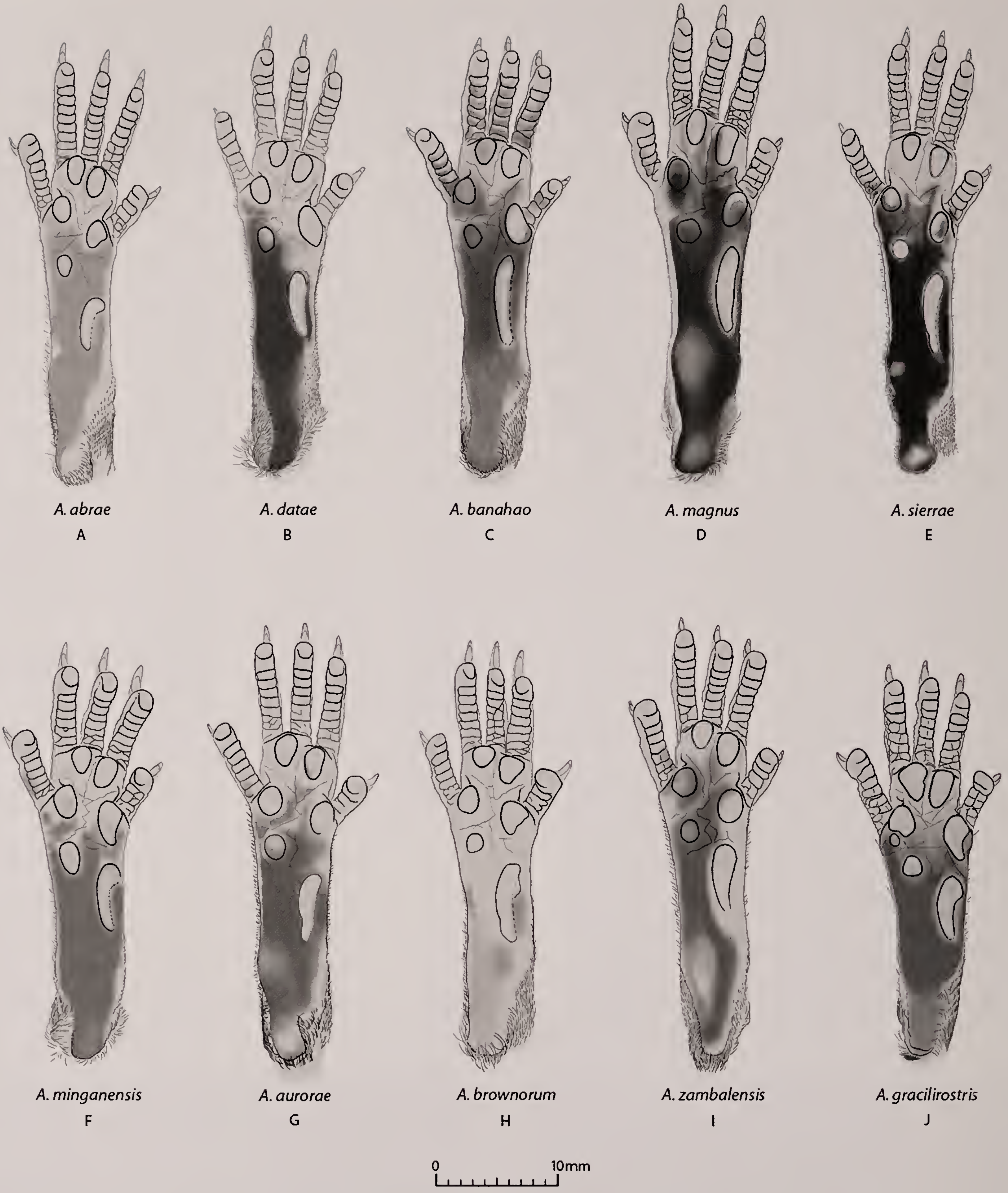
Apomys datae		*Apomys abrae*					
Mt. Pulag, Benguet Prov.		Massisiat, Abra Prov.		Mt. Data, Mountain Prov.		Balbalasang, 900 m, Kalinga Prov.	
M (n = 10)	F (n = 10)	M-holotype FMNH 62750	F (n = 1)	M (n = 2)	F (n = 4)	M (n = 1)	F (n = 1)
35.68 ± 0.61	35.19 ± 0.91	31.09	31.70	32.64 ± 0.90	32.40 ± 0.44	32.39	32.55
34.65–36.59	33.90–37.04	—	—	32.00–33.27	31.80–32.74	—	—
6.23 ± 0.28	6.00 ± 0.22	5.50	—	5.83 ± 0.25	5.69 ± 0.19	6.09	5.50
5.80–6.74	5.73–6.31	—	—	5.65–6.00	5.54–5.96	—	—
18.57 ± 0.47	18.45 ± 0.51	—	—	17.42 (1)	17.02 ± 0.30 (3)	16.74	16.81
18.12–19.50	17.68–19.47	—	—	—	16.84–17.37	—	—
14.69 ± 0.41	14.53 ± 0.27	—	—	13.73 ± 0.88	13.89 ± 0.35	13.29	13.50
14.20–15.42	14.11–14.92	—	—	13.10–14.35	13.52–14.35	—	—
14.75 ± 0.45	14.84 ± 0.58	12.59	13.03	13.39 ± 0.22	13.67 ± 0.40	14.05	13.64
14.21–15.65	13.54–15.41	—	—	13.23–13.54	13.26–14.11	—	—
5.26 ± 0.19	5.47 ± 0.22	4.60	4.75	5.07 ± 0.04	5.07 ± 0.21	5.09	4.79
4.95–5.51	5.18–5.96	—	—	5.04–5.10	4.88–5.36	—	—
7.63 ± 0.26	7.46 ± 0.38	6.39	6.55	7.09 ± 0.27	6.92 ± 0.21	6.82	7.05
7.38–8.23	6.89–7.95	—	—	6.90–7.28	6.67–7.18	—	—
16.59 ± 0.45	16.24 ± 0.60	13.62	14.17	15.20 ± 0.12	14.60 ± 0.56	14.93	14.66
15.93–17.38	15.40–17.19	—	—	15.11–15.28	14.10–15.19	—	—
11.64 ± 0.32	11.62 ± 0.36	10.84	—	10.75 ± 0.77	11.13 ± 0.20	11.00	11.26
11.01–12.14	10.99–12.00	—	—	10.20–11.29	10.86–11.30	—	—
7.09 ± 0.25	7.10 ± 0.28	6.69	6.62	6.68 ± 0.11	6.94 ± 0.08	6.54	7.09
6.71–7.46	6.48–7.57	—	—	6.60–6.75	6.85–7.01	—	—
7.49 ± 0.29	7.41 ± 0.27	6.75	—	6.97 ± 0.04	7.18 ± 0.12	7.13	7.14
7.00–7.93	7.10–7.93	—	—	6.94–7.00	7.08–7.33	—	—
9.72 ± 0.32	9.51 ± 0.30	7.79	8.62	8.68 ± 0.61	8.48 ± 0.19	8.83	8.33
9.30–10.28	9.05–9.94	—	—	8.25–9.11	8.31–8.75	—	—
11.86 ± 0.29	11.72 ± 0.44	10.62	—	11.36 ± 0.34	10.99 ± 0.15	11.77	11.68
11.54–12.28	11.10–12.37	—	—	11.12–11.60	10.83–11.18	—	—
5.23 ± 0.29	5.00 ± 0.26	4.23	—	4.82 ± 0.45	4.82 ± 0.34	4.67	4.96
4.72–5.65	4.57–5.44	—	—	4.50–5.13	4.44–5.14	—	—
11.13 ± 0.42	11.14 ± 0.37	10.43	—	10.03 ± 0.69	10.63 ± 0.43	10.47	10.57
10.57–11.95	10.55–11.66	—	—	9.54–10.52	10.09–11.03	—	—
1.92 ± 0.13	1.88 ± 0.09	1.93	1.78	1.71 ± 0.14	1.80 ± 0.03	1.83	1.81
1.71–2.13	1.74–2.03	—	—	1.61–1.81	1.77–1.83	—	—
2.24 ± 0.08	2.29 ± 0.13	2.06	2.09	1.99 ± 0.04	2.01 ± 0.05	2.08	2.05
2.08–2.40	2.08–2.50	—	—	1.96–2.01	1.95–2.05	—	—
3.63 ± 0.22	3.56 ± 0.24	3.01	3.15	3.10 ± 0.07	3.17 ± 0.21	3.13	3.22
3.22–3.94	3.16–3.92	—	—	3.05–3.15	2.90–3.36	—	—
143.8 ± 6.7	139.7 ± 7.4	125	139	136 (1)	133.0 ± 3.6 (3)	—	—
131–155	132–153	—	—	—	129–136	—	—
273.9 ± 9.2	268.5 ± 11.1	255	278	271 (1)	267.7 ± 5.9 (3)	—	—
261–292	255–287	—	—	—	261–272	—	—
130.1 ± 4.0	128.8 ± 6.3	130	139	135 (1)	134.7 ± 3.1 (3)	137	129
122–137	121–136	—	—	—	132–138	—	—
36.8 ± 1.0 (9)	35.9 ± 1.3	34	35	36 (1)	35.0 ± 0.0 (3)	35	35
35–38	35–39	—	—	—	35	—	—
22.1 ± 0.6	21.1 ± 1.0	-	—	21 (1)	20.7 ± 0.6 (3)	21	21
21–23	20–22	—	—	—	20–21	—	—
87.8 ± 10.6	77.2 ± 6.2 (9)	—	—	72 (1)	68.0 ± 8.5 (2)	—	—
70–105	70–86	—	—	—	62–74	—	—

Ilocos Norte Prov.: Mt. Simminublar (FMNH 92753–92756, 92758–92760, 92762); Mt. Simminublar, 4000 ft [ca. 1200 m] (FMNH 92757); Mt. Simminublar, 4300 ft [ca. 1300 m] (FMNH 92761); Mt. Simminublar, 4350 ft [ca. 1300 m] (FMNH 92752); Tagudin (AMNH 252473).

Kalinga Prov.: Balbalan Munic.: Balbalasang Brgy.: Balbalasang, 900 m (FMNH 169182, 169183); Balbalasang Brgy.: Magdallao, 1600 m (FMNH 167245, 167254, 167258, 167259, 167261–167262, 167273–167277, 167285–167287, 167292, 167294, 167299–167301, 167303, 167342–167344, 167346, 167347, 167349, 167355, 167356, 167358, 167361, 167367); Balbalan Munic.: Balbalasang Brgy.: Mapga, 1050 m (FMNH 169021–169067, 169069, 169070, 170904–170930).

Mountain Prov.: 0.3 km N Barlig Munic. Hall, 1730 m (FMNH 193532); 0.4 km N Barlig Munic. Hall, 1790 m (FMNH 193533, 193534, 193867, 193868); 0.6 km N Barlig Munic. Hall, 1800 m (FMNH 193535–193547, 193869–193876); Mt. Data (FMNH 62738); Mt. Data, 5300 ft [ca. 1600 m] (FMNH 62719, 62728); Mt. Data, 6500 ft [ca. 2000 m] (FMNH 62700); Mt. Data, 7500 ft [ca. 2300 m] (FMNH 62723–62724, 62726); 8000 ft [ca. 2400 m] (FMNH 62739, 62740); Mt. Data: 0.9 km N, 1.75 km E south peak, 2228 m (FMNH 188294–188297, 188483); Mt. Data: 1.0 km N, 1.25 km E south peak, 2231 m (FMNH 188292, 188293, 188437).

EMENDED DIAGNOSIS AND DESCRIPTION—A medium-sized *Megapomys*, averaging smaller than *A. datae* in nearly all measurements (Tables 2, 3). The tail is long relative to the head and body, with TV/HBL of our sampled populations averaging 97–101%. The dorsal pelage is a rich and dark brown, with little or no rusty-orange tint (Fig. 1C). The fur on the dorsal surface of the forepaws and hind feet is white or with very few scattered dark hairs (vs. having dark hairs extending over much of the tops of the feet). *Apomys abrae* rarely have any black hairs on the ventral surface of the tail,


A. abrae
A

A. datae
B

A. banahao
C

A. magnus
D

A. sierrae
E

A. minganensis
F

A. aurorae
G

A. brownorum
H

A. zambalensis
I

A. gracilirostris
J

Fig. 10. Ventral surface of the right hind feet of *Apomys* subgenus *Megapomys*, all shown to the same scale.

and the scales are white (when clean). The hind feet are proportionately somewhat narrow, the toes are long, and the plantar pads are relatively small and well separated (Fig. 10A). The ventral surface of the hind foot typically has little pigment. Specimens from Abra and Ilocos Norte have dorsal pelage much paler than specimens from Benguet, Kalinga, or Mountain province, approaching sandy-brown with orange tints. We suspect this is due to fading in these older specimens (1940s–1960s); field surveys in Abra and Ilocos Norte are needed to test this hypothesis.

The cranium of *A. abrae* (Fig. 16) is one of the smallest within *Megapomys*, with a moderately short and slender rostrum, rounded braincase, narrow palate, short maxillary toothrow, and short postpalatal region (Tables 2, 3). Its small size is clearly apparent on the first axis of the PCA of craniodental measurements, on which *A. abrae* and *A. brownorum* sp. nov. have the lowest scores (Fig. 6A). The foramen in the bulla for the stapedial artery is lacking in *A. abrae* (Fig. 5A); that is, it has the "abrae pattern" (see Carotid Circulatory Patterns above). The interparietal bone is variable in shape, but usually oval and, anteroposteriorly, relatively narrow. The mandible (Fig. 16C) is relatively small and slender, with a relatively short coronoid process, narrow angular process, and deeply concave margin between the condylar and angular processes.

The karyotype of *A. abrae*, based on two males from Kalinga Province (FMNH 169051, 169065), has 2n = 44, FN ≥ 54 (Fig. 8B). The autosomal complement includes two pairs of large submetacentric, two pairs of small to medium-sized subtelocentric, one pair of very small metacentric, and 16 pairs of telocentric (or subtelocentric) chromosomes. Both the large X chromosome and the very small Y are telocentric. This karyotype was mistakenly reported earlier as representing *A. datae* (Rickart & Heaney, 2002). The two species have very similar karyotypes, although there may be minor variation in the number and size of secondary arms on some autosomes. In contrast, both *A. zambalensis* sp. nov. and *A. banahao* sp. nov. have submetacentric X chromosomes and FN ≥ 58; the former has 2n = 44 and the latter 2n = 48.

To assess geographic variation among individuals we refer to this species, we conducted a PCA of the 18 craniodental measurements in Tables 2 and 3. This included specimens from Mt. Data (Mountain Province), from three elevations on Mt. Bali-it (Kalinga Province), and from Mt. Amuyao. Because the specimens from Abra (including the holotype) and Ilocos Norte provinces have damaged skulls, they could not be included in this analysis. The first component, which accounted for 34% of the variance, loaded heavily on most measurements, with the exception of orbitotemporal length, braincase height, and breadth of M^1 (Table 6). The second component, which accounted for 15% of the variance, loaded most heavily on length of the molar toothrow, palatal breadth at M^1, diastema length, braincase height, breadth of M^1, and width of the zygomatic plate. The remaining components had eigenvalues below 2.0 and were not interpretable. A plot of individual scores on PC1 and PC2 (Fig. 17) shows a high degree of overlap among the five groups, with no evident means to distinguish among them. Because we can detect no apparent differences among the crania of any of the specimens listed above as *A. abrae*, and because the cyt *b* data (Fig. 7) show specimens from Abra and Ilocos Norte provinces to be very similar to samples from Mt. Data and Mt. Amuyao, we conclude that these represent a single species.

COMPARISONS—As noted above, *A. abrae* differs from *A. datae* in being smaller overall, usually with little or no overlap in the features measured (Tables 2, 3), but the tail is proportionately longer (in our sampled populations, averaging 97–101% vs. 89–95% in *A. datae*), and a plot of relative length of the tail and weight (Fig. 12A) shows little overlap. The dorsal fur of *A. abrae* (Fig. 1C) has little of the rusty, slightly orange tint that *A. datae* (Fig. 1B) typically possesses. The tail of *A. abrae* is white ventrally, whereas scattered black hairs are often present on *A. datae*, and the scales are pale gray, not white. The toes of *A. abrae* are relatively longer and narrower than those of *A. datae*, the plantar pads are smaller and more widely separated than in *A. datae*, and much less pigment on the ventral surface is present than in *A. datae* (Fig. 10B). The cranium of *A. abrae* is consistently smaller than that of *A. datae*, with little overlap in zygomatic breadth, mastoid breadth, nasal length, rostral depth, rostral length, width of the zygomatic plate, and postpalatal length (Tables 2, 3). Bivariate plots of zygomatic breadth and mastoid breadth (Fig. 12B) and of rostral length and rostral depth (Fig. 12C) show the differences clearly. The interparietal bone of *A. abrae* is usually anteroposteriorly narrower than that of *A. datae*. The mandible of *A. datae* is larger and more robust, as described under that species.

Musser (1982) noted that morphological differences between *A. abrae* and *A. sacobianus* are slight in most respects and suggested that they might be conspecific. With our larger sample of *A. abrae*, it is clear that the holotype and still only known specimen of *A. sacobianus* is larger in all respects and differs in having a narrow line of dark hairs reaching to the base of the toes on the dorsal surface of the forefeet (vs. white fur only). The cranium is generally larger and more robust with a deeper and wider rostrum, but the palate is narrower. Additional details are discussed in the *A. sacobianus* species account below.

DISTRIBUTION—*Apomys abrae* occurs widely over the Central Cordillera of northern Luzon, with records from Benguet to Ilocos Norte (Figs. 3, 18). It has been recorded from 950 to 2200 m elevation (Fig. 15) in habitats ranging from mixed grass and shrubs beneath pines to dense montane rain forest. Compared with *A. datae*, with which it overlaps broadly, it often occurs at lower elevations and in relatively drier and more open habitats, including, but not restricted to, pine forest with broad-leafed undergrowth (Heaney et al., 1998, 2003; Rickart et al., 2007, 2011). Additional surveys are needed to determine its distribution at lower and middle elevations in Abra, Apayao, Ilocos Norte, and Ilocos Sur provinces in the Cordillera and at the boundary of the Central Cordillera and the Caraballo Mountains, where *A. sierrae sp. nov.* occurs.

COMMENTS—Given the conspicuous and easily recognized diagnostic features of this species, it is remarkable that the mitochondrial data (Fig. 7) fail to separate *A. abrae* and *A. datae*. We hypothesize that this is an instance of introgression because analysis of some nuclear genes reveals a subsample of individuals to be reciprocally monophyletic and not sister-species (S. J. Steppan, unpubl. data); details will be published elsewhere.

Apomys gracilirostris Ruedas, 1995

Apomys gracilirostris Ruedas, 1995: 305.

HOLOTYPE—NMP 3482. Adult male collected 12 June 1992. Field number NMP/CMNH 1136. Prepared as stuffed skin plus skull.

TYPE LOCALITY—Philippines: Mindoro Island: Mindoro Occidental Province: San Teodoro Munic.: North Ridge approach to Mt. Halcon, ca. 1580 m, ca. 13°16′48″N, 121°59′19″E.

SPECIMENS EXAMINED (n = 2): **MINDORO ISLAND**: Mindoro Occidental Prov.: San Teodoro Munic.: North Ridge approach to Mt. Halcon (NMP 3476, 3478).

EMENDED DIAGNOSIS AND DESCRIPTION—The pelage of this species both dorsally and ventrally is dark brown, but slightly paler ventrally (Fig. 1A). The tail is proportionately longer than in other *Megapomys*, averaging about 105% of head and

Table 3. Cranial and external measurements (mean ± 1 S.D. and range) of *Apomys abrae*, *A. gracilirostris*, *A. sacobianus*, and *A. brownorum*.

	Apomys abrae					
	Balbalasang, 1100 m, Kalinga Prov.		**Balbalasang, 1600 m, Kalinga Prov.**		**Mt. Amuyao, Mountain Prov.**	
Measurement	**M (n = 10)**	**F (n = 11)**	**M (n = 2)**	**F (n = 3)**	**M (n = 5)**	**F (n = 5)**
Basioccipital length	33.47 ± 0.59 32.62–34.32	32.86 ± 0.67 31.73–34.28	33.14 ± 0.87 32.52–33.75	33.02 ± 0.25 32.74–33.20	32.45 ± 0.37 32.00–32.97	33.42 ± 0.94 (4) 32.16–34.40
Interorbital breadth	5.72 ± 0.15 5.50–6.01	5.61 ± 0.15 5.42–5.95	5.69 ± 0.13 5.59–5.78	5.60 ± 0.16 5.46–5.78	5.60 ± 0.15 5.47–5.86	5.55 ± 0.07 5.43–5.60
Zygomatic breadth	17.41 ± 0.45 16.87–18.13	17.00 ± 0.34 16.53–17.69	16.83 ± 0.18 16.70–16.95	17.00 ± 0.47 (2) 16.66–17.33	16.56 ± 0.48 16.04–17.17	16.65 ± 0.35 16.19–16.98
Mastoid breadth	13.89 ± 0.28 (9) 13.45–14.30	13.73 ± 0.15 13.51–14.03	13.99 ± 0.06 13.95–14.03	13.53 ± 0.26 13.29–13.81	13.25 ± 0.33 12.88–13.74	13.38 ± 0.12 (4) 13.27–13.53
Nasal length	13.82 ± 0.34 13.24–14.15	13.61 ± 0.34 13.22–14.29	13.52 ± 0.06 13.48–13.56	13.78 ± 0.28 13.47–13.99	13.48 ± 0.24 13.24–13.83	13.93 ± 0.45 13.15–14.33
Incisive foramen length	5.05 ± 0.27 4.57–5.44	5.02 ± 0.23 4.61–5.41	5.31 ± 0.22 5.15–5.46	5.24 ± 0.35 4.91–5.60	5.07 ± 0.29 4.76–5.47	5.03 ± 0.24 4.80–5.34
Rostral depth	7.23 ± 0.15 7.06–7.56	7.10 ± 0.19 6.86–7.44	7.25 ± 0.07 7.20–7.30	7.09 ± 0.24 6.83–7.30	6.77 ± 0.15 6.62–7.02	6.98 ± 0.22 6.71–7.28
Rostral length	14.86 ± 0.29 14.42–15.28	14.52 ± 0.42 13.91–15.23	14.54 ± 0.10 14.47–14.61	14.74 ± 0.26 14.48–15.00	14.57 ± 0.22 14.33–14.92	14.99 ± 0.46 14.22–15.37
Orbitotemporal length	11.13 ± 0.35 10.57–11.82	11.14 ± 0.26 10.72–11.57	11.51 ± 0.57 11.10–11.91	10.95 ± 0.34 10.63–11.31	11.24 ± 0.29 10.80–11.50	11.50 ± 0.19 11.31–11.81
Maxillary toothrow length	6.93 ± 0.25 6.55–7.40	6.82 ± 0.21 6.56–7.23	7.05 ± 0.06 7.00–7.09	6.69 ± 0.07 6.61–6.74	6.69 ± 0.15 6.51–6.87	6.76 ± 0.09 6.65–6.89
Labial palatal breadth at M^1	7.27 ± 0.15 7.07–7.48	7.06 ± 0.19 6.72–7.33	7.20 ± 0.03 7.18–7.22	6.85 ± 0.09 6.79–6.95	7.06 ± 0.25 6.82–7.43	7.05 ± 0.19 6.79–7.30
Diastema length	9.04 ± 0.26 8.69–9.42	8.85 ± 0.36 8.14–9.32	8.72 ± 0.16 8.61–8.83	9.00 ± 0.30 8.65–9.18	8.86 ± 0.36 8.54–9.47	9.10 ± 0.16 8.93–9.34
Postpalatal length	11.77 ± 0.32 11.24–12.35	11.55 ± 0.20 11.20–11.87	11.44 ± 0.23 11.28–11.60	11.54 ± 0.10 11.42–11.60	10.86 ± 0.13 10.66–10.99	11.25 ± 0.76 (4) 10.34–12.15
Lingual palatal breadth at M^3	5.09 ± 0.14 (9) 4.90–5.34	4.89 ± 0.17 4.44–5.07	4.91 ± 0.21 4.76–5.05	4.93 ± 0.38 4.61–5.35	4.54 ± 0.23 4.29–4.78	4.96 ± 0.17 4.70–5.16
Braincase height	10.52 ± 0.36 10.07–11.12	10.46 ± 0.21 10.09–10.70	10.86 ± 0.08 10.80–10.91	10.43 ± 0.14 10.30–10.58	10.42 ± 0.33 9.92–10.71	10.33 ± 0.17 (4) 10.08–10.42
Breadth of M^1	1.82 ± 0.04 1.76–1.90	1.79 ± 0.09 1.61–1.91	1.80 ± 0.02 1.78–1.81	1.65 ± 0.06 1.60–1.72	1.84 ± 0.03 1.80–1.87	1.83 ± 0.05 1.79–1.89
Breadth of incisors at tip	2.15 ± 0.09 1.94–2.27	2.09 ± 0.07 1.99–2.24	2.15 ± 0.04 2.12–2.18	2.12 ± 0.02 2.10–2.14	1.96 ± 0.07 1.86–2.02	2.05 ± 0.10 1.89–2.12
Width of zygomatic plate	3.31 ± 0.11 3.08–3.44	3.23 ± 0.15 2.93–3.49	3.20 ± 0.13 3.10–3.29	3.36 ± 0.29 3.03–3.58	3.09 ± 0.09 3.00–3.21	3.03 ± 0.14 2.90–3.24
Length of head and body	134.6 ± 5.6 (9) 124–141	131.4 ± 5.0 (10) 121–137	131.5 ± 2.1 130–133	132.7 ± 1.2 132–134	126.2 ± 4.0 122–132	133.6 ± 4.7 126–137
Total length	269.6 ± 6.8 (9) 258–283	262.6 ± 8.6 242–275	259.0 ± 1.4 258–260	262.7 ± 4.6 260–268	254.0 ± 8.6 242–265	264.2 ± 7.8 252–272
Length of tail vertebrae	135.9 ± 6.7 125–144	130.8 ± 6.3 (10) 121–140	127.5 ± 0.7 127–128	130.0 ± 3.5 128–134	127.8 ± 4.9 120–133	130.6 ± 3.9 126–135
Length of hind foot	37.0 ± 0.7 (9) 36–38	35.8 ± 1.4 (10) 34–39	36.0 ± 0.0 36	35.7 ± 0.6 35–36	34.4 ± 0.5 34–35	34.2 ± 1.1 33–35
Length of ear	22.0 ± 0.5 (9) 21–23	21.6 ± 0.5 (10) 21–22	23.0 ± 1.4 22–24	22.7 ± 0.6 22–23	21.4 ± 0.5 21–22	21.2 ± 0.4 21–22
Weight (g)	72.6 ± 4.7 (9) 66–79	66.7 ± 6.5 (10) 59–76	71.5 ± 3.5 69–74	57.0 ± 4.6 53–62	56.6 ± 5.9 50–66	62.6 ± 5.2 54–68

body length (Ruedas, 1995), and is thicker at the base than in other species. The tail is dark brown both dorsally and ventrally, slightly paler ventrally, and often white at the tip. The hind feet are shorter and broader than those of other *Megapomys*, with proportionately larger plantar pads and a hallux that reaches to the top or slightly beyond the top of the adjacent plantar pad; the ventral surface is moderately heavily pigmented except for the pads (Fig. 10J; Table 3). The upper incisors are laterally compressed relative to depth, 1.56–1.76 mm at the tip; the lower incisors are unpigmented and elongate (Fig. 19). The rostrum is long and slender and turns up slightly near the tip. The braincase is more globose than in other *Megapomys*. The maxillary molars are narrow and the toothrow is short. The postpalatal region is long. A foramen is present in the bulla for the stapedial artery (the "datae pattern"). The interparietal bone is variable in shape but is usually moderately wide anteroposteriorly. The mandible (Fig. 19C) is long and slender, with a short coronoid process and a short, blunt angular process (see Ruedas [1995] for additional details). No other species of rodent on Mindoro is similar in size and overall morphology.

Comparisons—*Apomys gracilirostris* differs from *A. datae* in having darker pelage dorsally and much darker pelage ventrally, with a proportionately longer and thicker tail and shorter and broader hind feet. The crania are of similar total length, but that of *A. datae* is more robust overall, with a

Table 3. *Extended.*

Apomys abrae	*Apomys gracilirostris*	*Apomys sacobianus*	*Apomys brownorum*		
Mt. Simminublan, Ilocos Norte Prov.	**Mt. Halcon, Mindoro Island**	**Sacobia River, Pampanga Prov.**	**Mt. Tapulao, 2024 m, Zambales Prov.**		
M/F (n = 9)	**F (n = 2)**	**M-holotype USNM 304352**	**M-holotype FMNH 183524**	**M (n = 10)**	**F (n = 5)**
32.10 ± 0.46 (5)	33.85 ± 0.71	34.29	33.57	33.55 ± 0.91	32.43 ± 0.33
31.43–32.58	33.34–34.35	—	—	32.41–34.85	31.96–32.75
5.48 ± 0.16 (7)	6.02 ± 0.21	6.02	5.75	5.65 ± 0.13	5.60 ± 0.13
5.27–5.71	5.87–6.17	—	—	5.38–5.87	5.46–5.78
16.65 ± 0.52 (4)	17.57 ± 0.20	17.97	17.54	17.44 ± 0.45	17.14 ± 0.24
15.93–17.17	17.43–17.71	—	—	16.69–18.09	16.88–17.45
13.17 ± 0.83 (3)	14.48 ± 0.04	14.04	14.01	14.09 ± 0.33	13.91 ± 0.26 (4)
12.21–13.65	14.45–14.51	—	—	13.63–14.70	13.69–14.28
13.18 ± 0.50 (8)	14.42 ± 0.28	13.91	13.62	13.88 ± 0.49	13.17 ± 0.31
12.18–13.70	14.22–14.62	—	—	12.90–14.63	12.74–13.58
5.08 ± 0.19 (8)	4.77 ± 0.13	5.70	4.86	5.03 ± 0.23	4.99 ± 0.16
4.89–5.52	4.67–4.86	—	—	4.66–5.48	4.80–5.16
6.85 ± 0.17 (7)	7.00 ± 0.11	7.96	7.06	7.05 ± 0.17	6.79 ± 0.16
6.62–7.11	6.92–7.08	—	—	6.73–7.36	6.54–6.97
14.22 ± 0.43 (7)	16.08 ± 0.55	15.04	14.92	15.12 ± 0.54	14.65 ± 0.25
13.60–14.68	15.69–16.47	—	—	14.27–15.83	14.28–14.93
11.24 ± 0.40 (4)	10.53 ± 0.23	11.73	11.59	11.28 ± 0.33	11.14 ± 0.34
10.81–11.77	10.36–10.69	—	—	10.63–11.70	10.81–11.58
6.59 ± 0.27 (7)	6.25 ± 0.09	6.92	6.53	6.59 ± 0.17	6.60 ± 0.18
6.19–6.99	6.19–6.31	—	—	6.37–6.81	6.38–6.80
6.79 ± 0.35 (5)	7.33 ± 0.01	7.20	6.87	6.82 ± 0.20	6.75 ± 0.10
6.42–7.31	7.32–7.34	—	—	6.56–7.09	6.57–6.83
8.47 ± 0.36 (7)	9.52 ± 0.54	8.55	9.44	9.44 ± 0.29	8.89 ± 0.16
7.98–8.98	9.13–9.90	—	—	8.79–9.77	8.67–9.09
10.99 ± 0.53 (4)	11.53 ± 0.27	11.88	11.66	11.51 ± 0.42	10.95 ± 0.18
10.26–11.42	11.34–11.72	—	—	11.03–12.10	10.75–11.21
4.51 ± 0.08 (2)	5.27 ± 0.01	4.10	4.80	4.87 ± 0.26	4.69 ± 0.30
4.45–4.56	5.26–5.27	—	—	4.46–5.29	4.35–5.05
10.23 ± 0.66 (3)	10.71 ± 0.71	10.30	11.13	10.65 ± 0.38	10.72 ± 0.34
9.50–10.76	10.20–11.21	—	—	10.12–11.13	10.32–11.25
1.72 ± 0.10 (7)	1.76 ± 0.01	1.97	1.76	1.69 ± 0.05	1.71 ± 0.06
1.58–1.85	1.75–1.77	—	—	1.63–1.76	1.65–1.79
2.06 ± 0.09 (7)	1.74 ± 0.03	2.27	2.13	2.09 ± 0.08 (9)	2.03 ± 0.07
1.93–2.23	1.72–1.76	—	—	1.94–2.18	1.92–2.08
3.08 ± 0.19 (8)	3.28 ± 0.12	3.46	2.70	2.71 ± 0.09	2.55 ± 0.20
2.84–3.33	3.19–3.36	—	—	2.56–2.82	2.23–2.78
—	—	141	135	134.3 ± 5.3 (9)	128.0 ± 4.6
—	—	—	—	125–140	123–135
—	—	290	250	246.9 ± 6.3 (9)	238.6 ± 6.2
—	—	—	—	235–255	230–247
—	147.0 ± 8.5	149	115	112.6 ± 2.7 (9)	110.6 ± 2.6
—	141–153	—	—	110–116	107–114
—	36.0 ± 0.0	40	34	33.8 ± 1.3	33.4 ± 1.5
—	36	—	—	32–36	31–35
—	18.0 ± 0.0	22	21	21.5 ± 0.5	21.6 ± 0.5
—	18	—	—	21–22	21–22
—	—	—	71	77.1 ± 5.5	69.4 ± 8.9
—	—	—	—	69–84	60–82

heavier rostrum, broader and more squarish braincase, broader zygomatic plate and zygomatic arches, broader incisive foramina, and a longer toothrow. Both species have the "datae pattern" of carotid circulatory pattern (Fig. 5). The mandible of *A. gracilirostris* is similar in length to that of *A. datae* but is more slender, with the bony sheath of the anterior portion of the mandible extending less far onto the incisor. The coronoid process of the mandible is shorter and less pointed than in *A. datae*, and the angular process is shorter and blunter.

Distribution—*Apomys gracilirostris* is currently known only from 1250 to 1950 m on the North Ridge of Mt. Halcon (Fig. 18). This species should be sought widely in the mountains that make up the central core of Mindoro, at elevations from 700 m to more than 2000 m, areas from which no data on small mammals are currently available. The long tail and short, broad hind foot implies to us that it could be partially arboreal.

Comments—The combination of the dark pelage, long tail, short and broad hind feet, and slender rostrum, globose braincase, and narrow incisors easily distinguish *A. gracilirostris* from all other *Megapomys*. The long tail and slender rostrum are characters shared with the subgenus *Apomys*, which suggests that they represent primitive character states, whereas the short tail and robust rostrum of the remaining species of *Megapomys* might represent shared, derived characters.

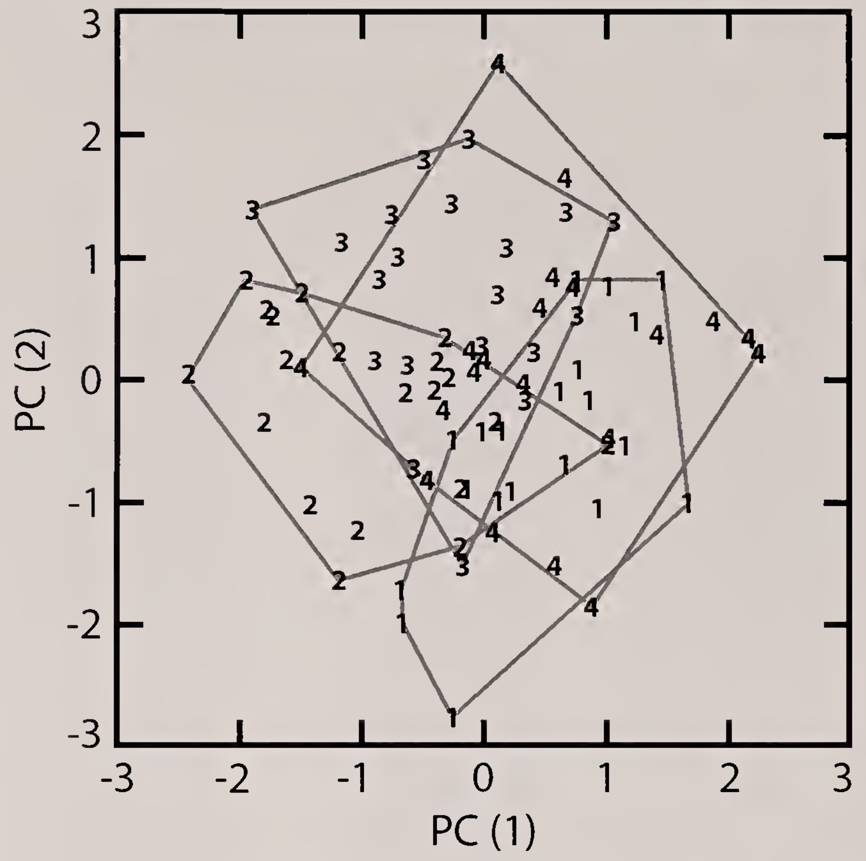


Fig. 11. Results of the principal components analysis of *Apomys datae* (see text and Table 4) based on specimens included in Table 2. 1 = Mt. Data, Mountain Province; 2 = Mt. Bali-it and vicinity, Kalinga Province; 3 = Mt. Amuyao, Mountain Province; 4 = Mt. Pulag, Benguet Province.

Apomys sacobianus Johnson, 1962

Apomys sacobianus Johnson, 1962: 317–319.

Holotype—usnm 304352. Adult male, collected 16 August 1956. Field number D. H. Johnson 8555. Prepared as stuffed skin plus skull. Measurements in Table 3.

Type Locality—Philippine Islands: Luzon: Pampanga Province: Clark Air Base, Sacobia River, in a narrow forested canyon of the Sacobia River "just above the point where it emerges from the foothills of the Zambales Mountains onto the plains of Pampanga" (Johnson, 1962: 319).

Table 4. Character loadings, eigenvalues, and percent variance explained on the first four components of a principal components analysis of log-transformed measurements of adult *Apomys datae* (see Fig. 11 and Methods).

Variable	Principal component			
	1	2	3	4
Basioccipital length	0.879	0.253	0.168	0.011
Interorbital breadth	0.454	0.145	−0.527	−0.228
Zygomatic breadth	0.725	−0.131	−0.211	0.325
Mastoid breadth	0.788	−0.010	−0.281	−0.128
Nasal length	0.767	0.190	0.034	−0.152
Incisive foramen length	0.036	0.397	0.433	0.518
Rostral depth	0.730	0.042	−0.105	0.162
Rostral length	0.778	0.193	0.150	−0.312
Orbitotemporal length	0.381	−0.230	−0.302	0.619
Maxillary toothrow length	0.591	−0.537	0.402	−0.157
Labial palatal breadth at M^1	0.581	−0.213	0.308	−0.307
Diastema length	0.611	0.598	0.093	0.097
Postpalatal length	0.693	0.051	0.056	−0.004
Lingual palatal breadth at M^3	0.431	0.466	−0.129	−0.152
Braincase height	0.495	−0.343	−0.510	0.069
Breadth of M^1	0.507	−0.660	0.311	−0.153
Breadth of incisors at tip	0.309	−0.339	−0.092	0.398
Width of zygomatic plate	0.358	0.029	0.466	0.409
Eigenvalue	6.451	1.969	1.610	1.477
Percent variance explained	35.84	10.94	8.95	8.21

Table 5. Character loadings, eigenvalues, and percent variance explained on the first four components of a principal components analysis of log-transformed measurements of adult *Apomys abrae* and *A. datae* (see Fig. 13 and Methods).

Variable	Principal component			
	1	2	3	4
Basioccipital length	0.937	0.144	0.123	0.010
Interorbital breadth	0.686	0.094	−0.344	−0.137
Zygomatic breadth	0.902	0.071	−0.135	0.110
Mastoid breadth	0.871	0.017	−0.192	−0.112
Nasal length	0.843	0.035	0.033	−0.074
Incisive foramen length	0.241	0.455	0.557	0.473
Rostral depth	0.861	0.122	−0.050	−0.096
Rostral length	0.884	0.059	0.068	−0.074
Orbitotemporal length	0.587	−0.005	−0.281	0.444
Maxillary toothrow length	0.543	−0.645	0.274	−0.060
Labial palatal breadth at M^1	0.646	−0.400	0.283	−0.236
Diastema length	0.738	0.455	0.174	0.054
Postpalatal length	0.690	0.051	0.129	−0.203
Lingual palatal breadth at M^3	0.512	0.315	0.071	−0.575
Braincase height	0.663	−0.159	−0.512	0.183
Breadth of M^1	0.468	−0.745	0.171	0.151
Breadth of incisors at tip	0.695	−0.046	−0.087	0.238
Width of zygomatic plate	0.694	−0.014	0.185	0.203
Eigenvalue	9.173	1.730	1.127	1.072
Percent variance explained	50.96	9.61	6.26	5.96

Specimens Examined—The holotype (and only known specimen).

Emended Diagnosis and Description—A large *Megapomys*, within the range of large individuals of *A. datae*, but larger than *A. abrae*. The tail is slightly longer than the length of head and body (149 mm/141 mm = 106%). The dorsal pelage is shorter and less dense than that of other *Megapomys* and grayish-brown rather than dark brown with red, orange, or yellow tones. The ventral pelage is pale whitish-gray, creamy along the midline and throat. The dorsal surfaces of the hind feet are white. The dorsal surfaces of the forefeet have a narrow stripe of dark hairs reaching from the forearm to the base of the central toes. Because the holotype is a dried museum study skin, no description of the ventral surface of the hind feet is possible, beyond noting that they are longer than those of most species of *Megapomys* (Table 3). The tail is sharply bicolored, dark grayish-brown dorsally and nearly white ventrally. The cranium (Fig. 20) is large and robust, with a deep, squarish braincase and a broad, deep rostrum. The incisive foramina are long (5.8 mm), as is the upper toothrow (7.1 mm). The palate is narrow, with the premaxillary toothrows diverging only slightly posteriorly. The postpalatal region is of moderate length. There is no foramen in the bulla for the stapedial artery (the "abrae pattern"; Fig. 5). The interparietal bone is of moderate anteroposterior width. The mandible (Fig. 20C) is of moderate length and is robust overall. The coronoid process is short, sturdy, and sharply pointed, and the angular process is deep and moderately pointed.

Comparisons—Because only the holotype is known, and usnm policy does not allow destructive sampling of holotypes, no material is available for genetic analysis. Here, we make comparisons to the four geographically nearest and most morphologically similar species.

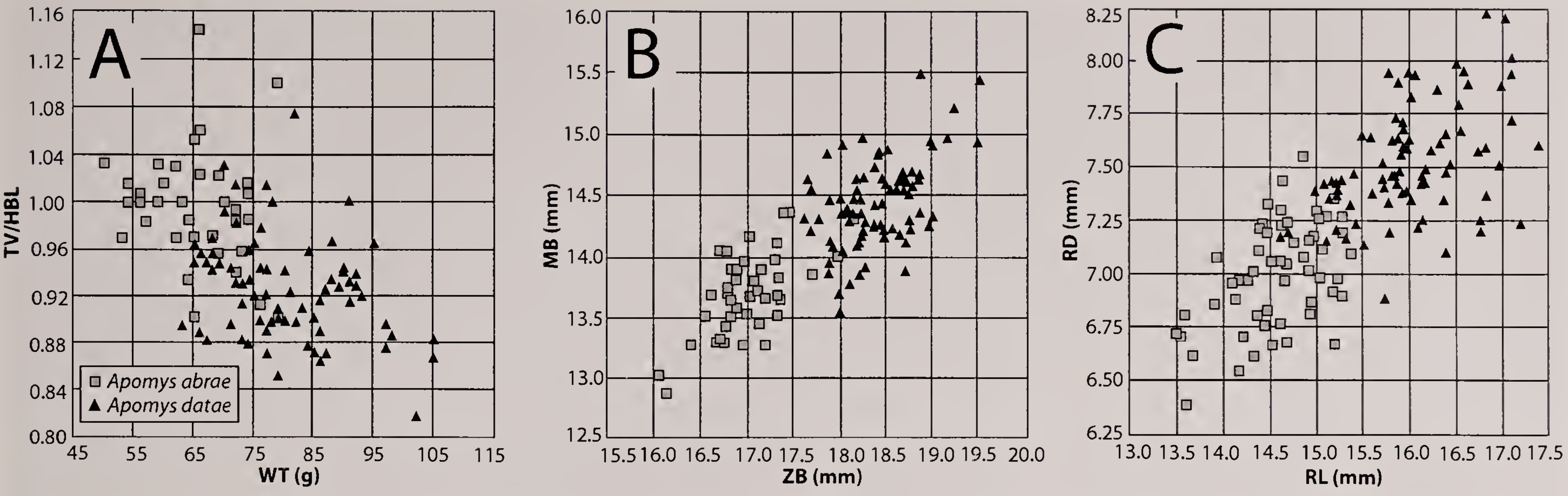


FIG. 12. Bivariate plots of measurements comparing *Apomys abrae* and *A. datae*. (**A**) Weight (WT) and length of tail vertebrae (TV) divided by length of head and body (HBL). (**B**) Zygomatic breadth (ZB) and mastoid breadth (MB). (**C**) Rostral length (RL) and rostral depth (RD).

Apomys sacobianus differs from *A. datae* in having shorter, relatively grayer dorsal pelage (vs. longer, softer, denser, and dark brown), with entirely white fur on the dorsal surface of the hind feet (vs. brown on the proximal portion). The tail is both absolutely (Fig. 21A) and proportionately longer (106% vs. 89–95%), and more sharply bicolored than is typical for *A. datae*. The length of the hind foot is greater than recorded for any *A. datae* (Fig. 21A). *Apomys sacobianus* has the carotid circulatory pattern of *A. abrae*, lacking a foramen in the bulla for a stapedial artery. The length of the incisive foramina is at the upper end of the range for *A. datae* (5.8 vs. ca. 4.6–5.8 mm), and the incisive foramina (Fig. 20B) are slightly narrower than is typical for *A. datae*. The length of the nasals is near the bottom of the range for *A. datae* (13.9 vs. 13.6–15.3 mm). The rostrum is deeper than all but the largest *A. datae* (Fig. 21B), but the rostral length is less than all but the smallest *A. datae*. Braincase height is less than in most *A. datae* (Fig. 21B), and diastema length is less than in all *A. datae* (Fig. 21C). The lingual breadth of palate at M^3 is also substantially less than in *A. datae* (Fig. 21C). Most other cranial measurements fall within the range for *A. datae*. The shape of the interparietal bone in the two species appears similar. The mandible (Fig. 20C) is similar to that of *A. datae*, although slightly more robust and with slightly shorter and more robust coronoid and angular processes.

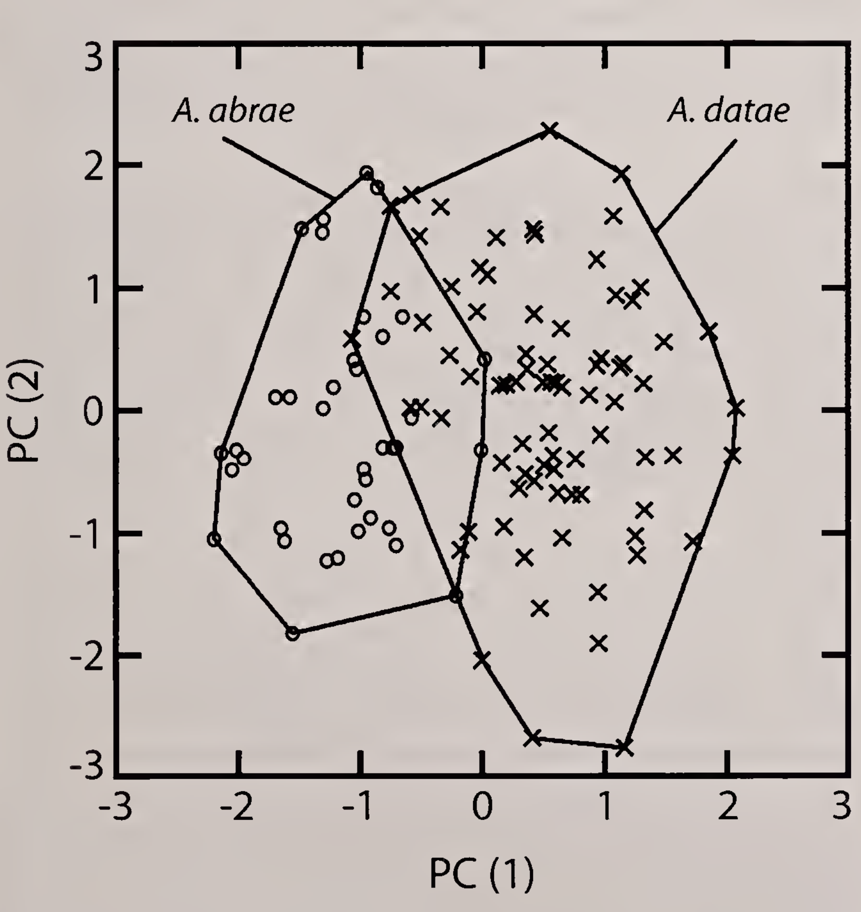


FIG. 13. Results of the principal components analysis of *Apomys datae* and *A. abrae* (see text and Table 5) based on specimens in Tables 2 and 3.

Apomys sacobianus differs from *A. abrae* in being larger in all respects, with virtually no overlap (Tables 2, 3). The pelage is longer and denser in *A. abrae*, with more extensive brown tints. They have tails of similar proportional length (106% vs. 90–115% of head and body length). The tail and hind foot are longer in *A. sacobianus* than in *A. abrae* (Fig. 21A). Both have white fur on the dorsal surface of the hind feet, but on the dorsal surface of the forefeet, *A. sacobianus* has a narrow line of dark hairs reaching from the forearm to the base of the toes, whereas the forefeet of *A. abrae* are entirely white. The cranium is larger and more robust overall, with an especially more robust (deeper and wider) rostrum (Fig. 21B). The incisive foramina of the one known specimen of *A. sacobianus* are narrower, and may be longer, than is typical for *A. abrae*, and the postpalatal length is greater. The lingual breadth of palate at M^3 is narrower than in *A. abrae* (Fig. 21C), which reflects the generally narrower palate of *A. sacobianus*. As noted by Musser (1982), the carotid circulation pattern in *A. sacobianus* is identical to that in *A. abrae*. The shape of the interparietal bone in the two species appears similar, although that of *A. sacobianus* is wider anteroposteriorly. The mandible of *A. sacobianus* (Fig. 20C) is larger and slightly more robust than that of *A. abrae*, with a less deeply concave posterior margin between the condylar and angular processes.

Apomys sacobianus differs from *A. zambalensis* sp. nov., which occurs nearby in the Zambales Mountains, in having grayish dorsal pelage (vs. rusty-orange brown) and in lacking the stapedial artery foramen in the bullae (which is present in all 53 *A. zambalensis* sp. nov. crania available). The holotype of *A. sacobianus* has a hind foot length that lies at the upper extreme of the range for *A. zambalensis* and a tail that is near the upper extreme for *A. zambalensis* sp. nov. (Fig. 22A). The crania differ conspicuously in several ways. Diastema length of *A. sacobianus* is much less than in *A. zambalensis* sp. nov., and braincase height falls near the lower extreme of the range for *A. zambalensis* sp. nov. (Fig. 22B). The length of M^1 to M^3 is below the lower end of the range for *A. zambalensis* sp. nov., and the lingual breadth of the palate at M^3 is conspicuously

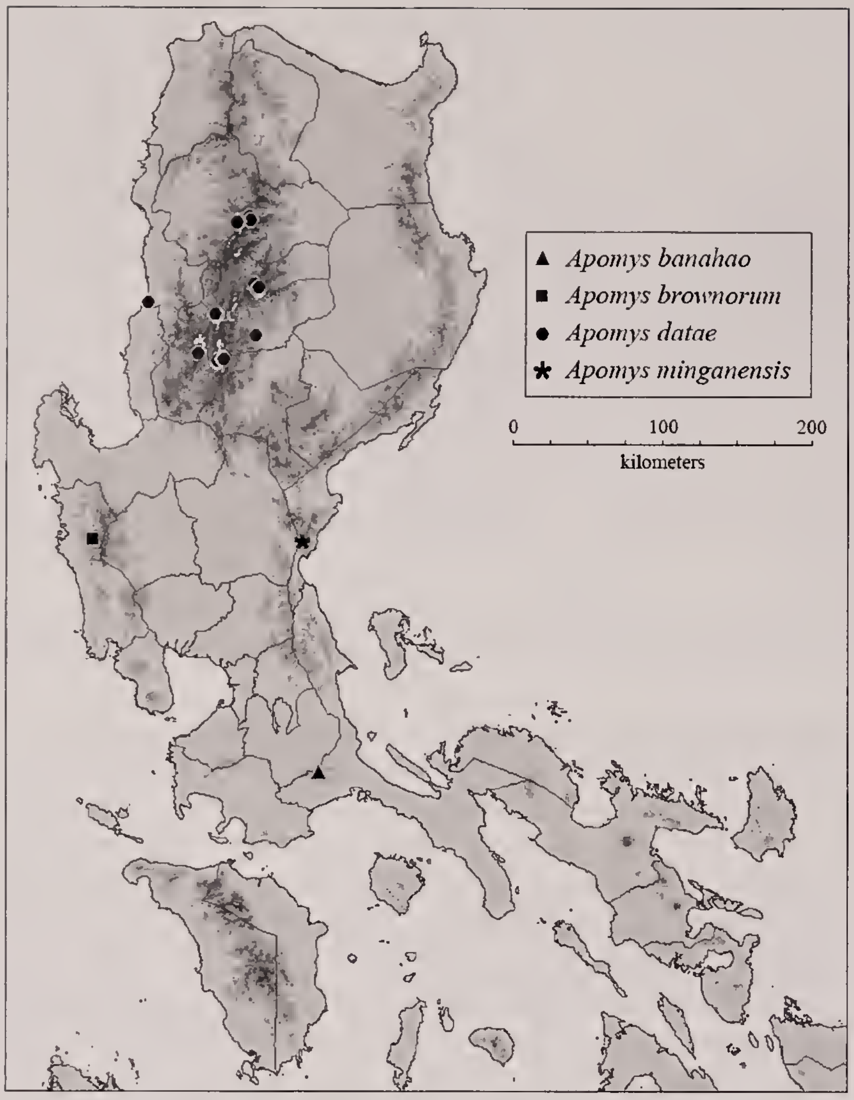


FIG. 14. Map showing the documented distribution of *Apomys banahao* sp. nov., *A. brownorum* sp. nov., *A. datae*, and *A. minganensis* sp. nov. See respective species accounts for localities. Shading on land areas, in increasingly dark tones of gray: 0–500 m elevation; 501–1000 m; 1001–1500 m; 1501–2000 m; and white above 2000 m. Provincial boundaries are shown for reference.

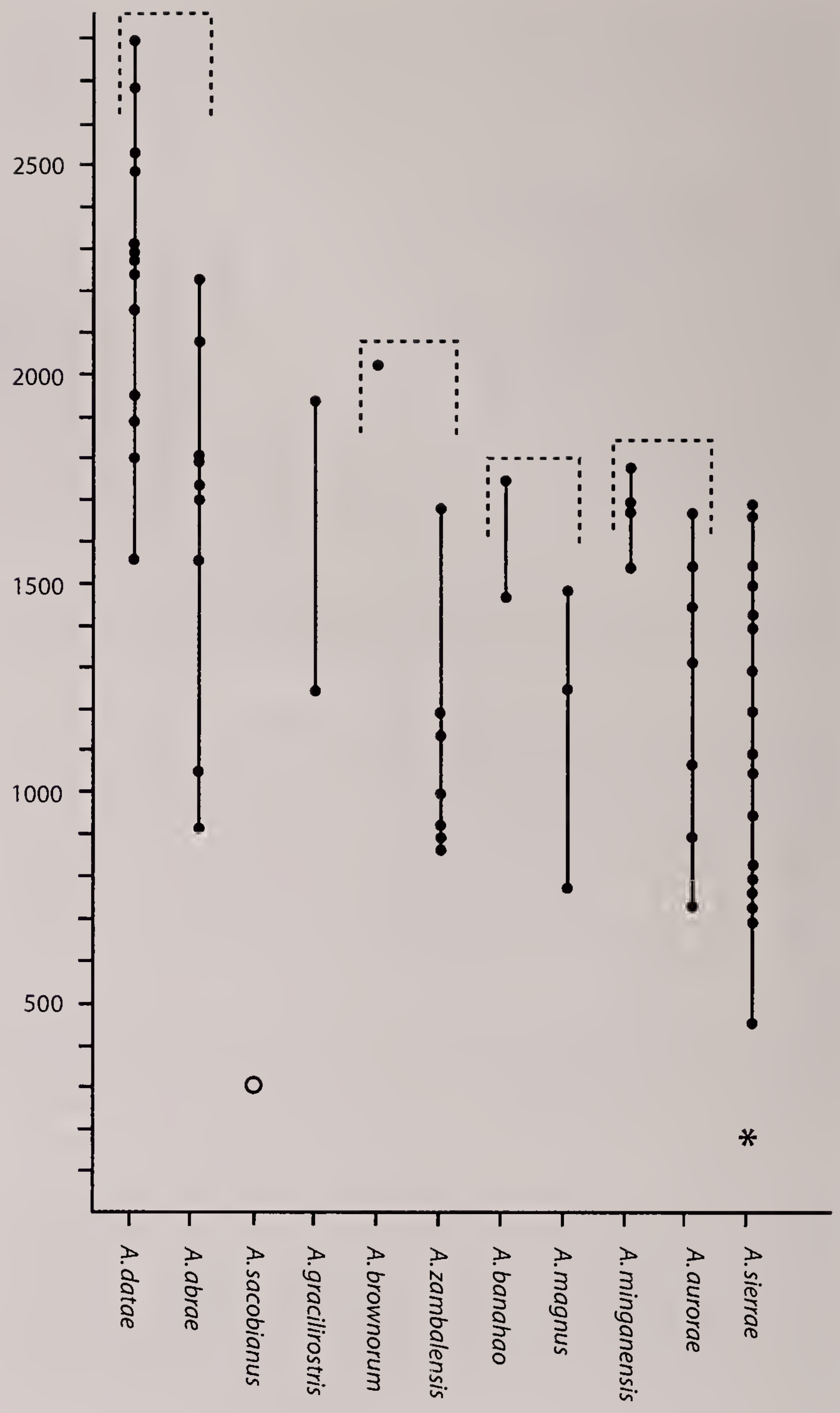


FIG. 15. Documented elevational ranges of the species of the subgenus *Megapomys* on Luzon. Brackets indicate regionally sympatric species. **Solid circle** = known elevation; **open circle** = estimated elevation (see text); **asterisk** = record from Palaui Island.

less (Fig. 22C). Additionally, the breadth of M^1 is greater in *A. sacobianus*, although only slightly so (2.0 vs. 1.6–1.9 mm; Tables 2, 3). In other cranial measures, the holotype of *A. sacobianus* falls within the range of *A. zambalensis* sp. nov. (Tables 2, 3). The interparietal bone of *A. sacobianus* is narrower than that of *A. zambalensis* sp. nov. The mandible of *A. zambalensis* sp. nov. is similar to that of *A. sacobianus*, but the posterior margin between the condylar and angular processes is narrower and more deeply concave.

Apomys magnus sp. nov. is substantially larger than *A. sacobianus* in all features measured (Tables 3, 12) and differs from it in the same specific details that separate *A. sacobianus* and *A. zambalensis* sp. nov.

To further assess the extent to which *A. sacobianus* differs from *A. zambalensis* sp. nov. and *A. magnus* sp. nov., we conducted a PCA of 18 craniodental measurements of these three species and also included *A. aurorae* sp. nov., which is geographically more distant from *A. sacobianus*, but which is a member of the same clade (Fig. 7). The first component, which accounted for 45% of the total variance, loaded heavily on all measurements except width of zygomatic plate (Table 7). The second component, which accounted for 12% of the variance, loaded heavily and positively on diastema length and postpalatal length, and heavily but negatively on interorbital breadth, palatal breadth at M^1, breadth of M^1, and width of the zygomatic plate. The remaining components had eigenvalues below 1.5 and were not interpretable. A plot of PC1 and PC2 (Fig. 23) showed the holotype (and sole known specimen) of *A. sacobianus* with a strongly negative score on the first axis, indicating its small size relative to the other included species. It lies outside of the polygons of *A. zambalensis* sp. nov. and *A. aurorae* sp. nov., for both of which we have good samples; because the holotype is a fully adult animal, this suggests that the size difference is likely to remain consistent when more specimens are obtained. *Apomys magnus* sp. nov. has the highest scores on the first axis, reflecting its large size.

On the second component, *A. sacobianus* had an intermediate score (Fig. 23), with most specimens of *A. zambalensis* sp. nov. scoring positively and most specimens of *A. aurorae* sp. nov. scoring negatively, reflecting differences in craniodental proportions that are more fully discussed below. *Apomys magnus* sp. nov. scored at intermediate to negative levels on this component, overlapping with *A. sacobianus* in this respect. We conclude that this analysis supports the recognition of all four of these species as being distinct from each other.

DISTRIBUTION—*Apomys sacobianus* is currently known only from the holotype, taken on the lower east-facing slope of the

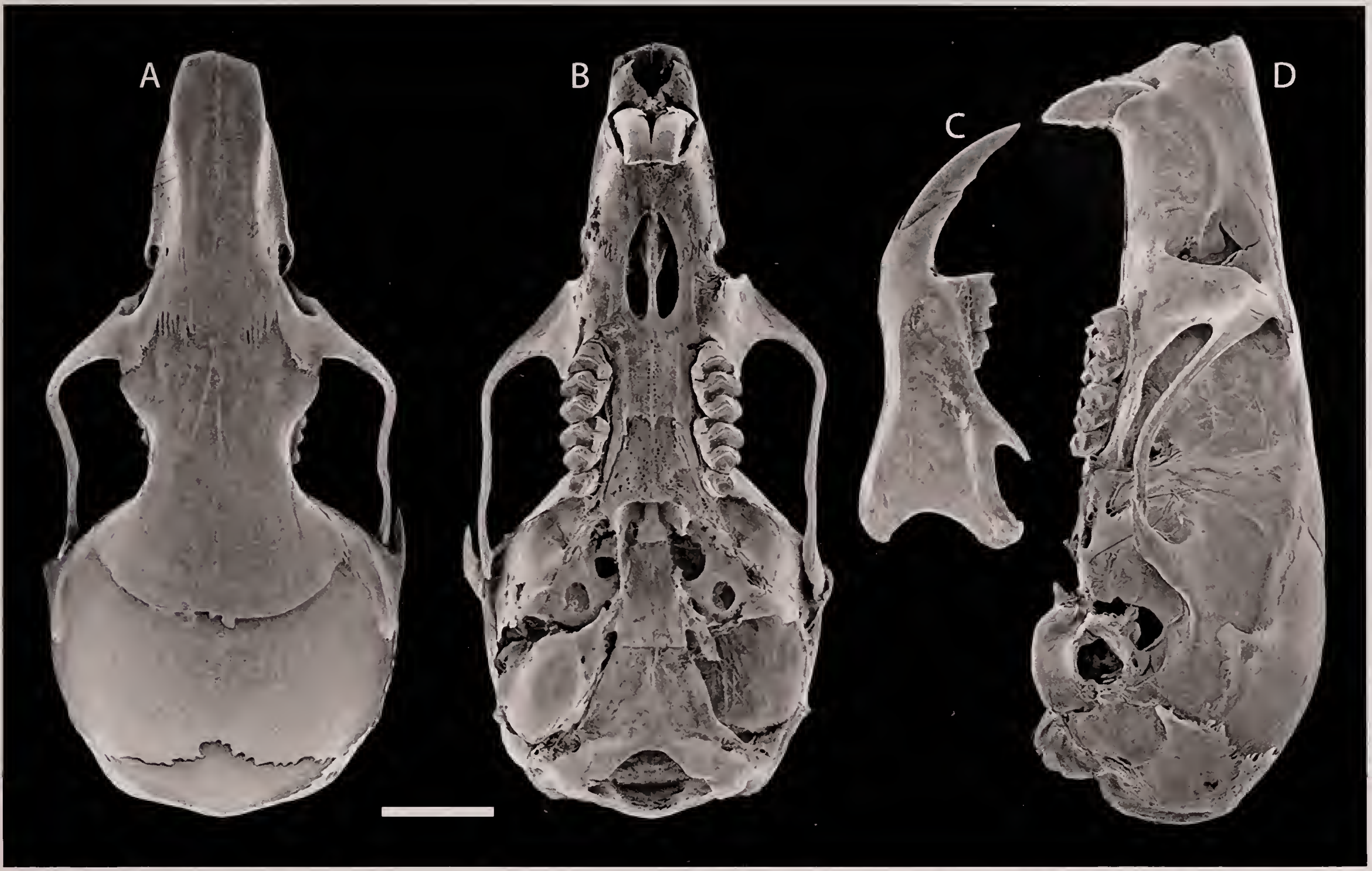


FIG. 16. Dorsal (**A**), ventral (**B**), and lateral (**D**) views of the cranium and lateral view of the mandible (**C**) of *Apomys abrae* (FMNH 62750, holotype); scale bar = 5 mm.

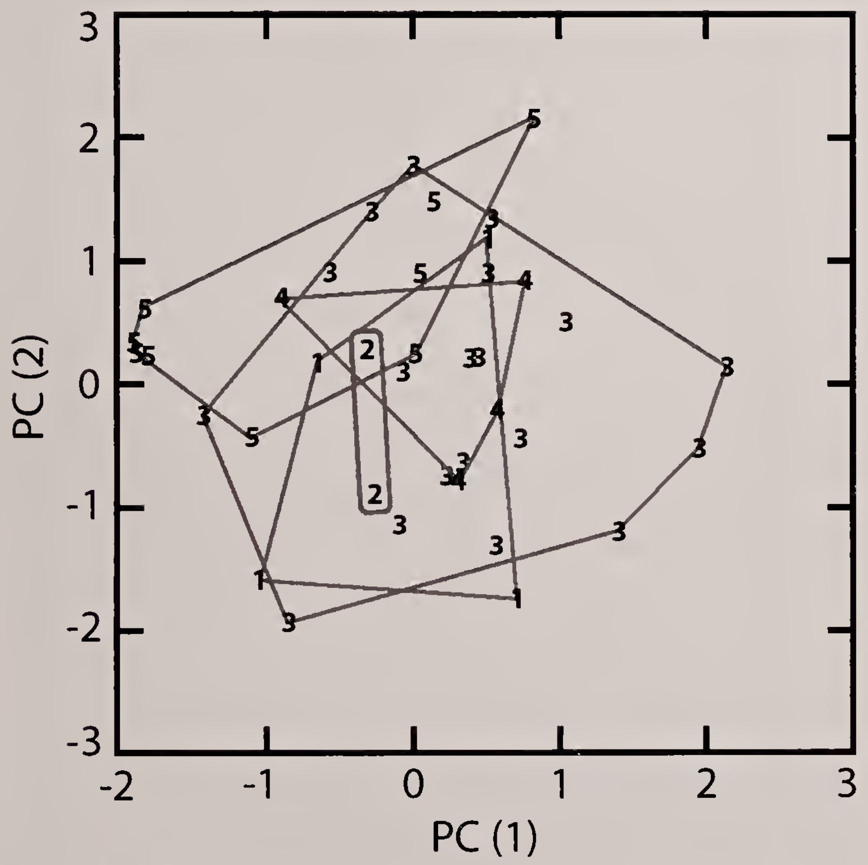


FIG. 17. Results of the principal components analysis of *Apomys abrae* (see text and Table 6) based on specimens included in Tables 2 and 3. 1 = Mt. Data, Mountain Province; 2 = Mt. Bali-it, Kalinga Province, 900 m; 3 = Mt. Bali-it, Kalinga Province, 1100 m; 4 = Mt. Bali-it, 1600 m, Kalinga Province; 5 = Mt. Amuyao, Mountain Province.

Zambales Mountains (Johnson, 1962; Fig. 18). We estimate the elevation of the type locality as roughly 300 m (Fig. 15). Because the species is known only from the holotype, the extent of the distribution is uncertain. It should be sought in the foothills of the Zambales Mountains in Pampanga, Tarlac, and Pangasinan provinces.

COMMENTS—Because *A. sacobianus* is known only from the holotype, an adult animal with moderately worn molars, the extent of variation is unknown, and no tissues are available for genetic study, making it impossible to adequately place this animal in the context of the other species treated here. Musser (1982) viewed *A. sacobianus* as a larger version of *A. abrae* but retained it as a species to emphasize the difference in size and to draw attention to the need for further study. We agree that they are similar and might be closely related, but we document here that there is indeed no overlap in cranial or external dimensions with our large sample of *A. abrae*. We also note the similarity in size with *A. zambalensis*, but the two differ in their types of carotid circulatory patterns and in numerous other cranial features, as listed above. Clearly, further study is needed, but we agree with Musser (1982) that maintaining this as a valid species is the best course of action. Further field surveys and more specimens are badly needed.

Apomys (*Megapomys*) *brownorum* sp. nov.

HOLOTYPE—FMNH 183524, adult male collected on 12 January 2005 by Danilo S. Balete, field number DSB 3531. A sample of muscle tissue was removed from the thigh in the

TABLE 6. Character loadings, eigenvalues, and percent variance explained on the first four components of a principal components analysis of log-transformed measurements of adult *Apomys abrae* (see Fig. 17 and Methods).

Variable	Principal component			
	1	2	3	4
Basioccipital length	0.784	0.390	0.225	0.063
Interorbital breadth	0.412	−0.285	−0.143	0.202
Zygomatic breadth	0.769	−0.077	−0.191	−0.037
Mastoid breadth	0.702	−0.264	−0.429	0.186
Nasal length	0.621	0.169	0.562	0.024
Incisive foramen length	0.362	0.470	−0.142	0.292
Rostral depth	0.832	0.107	−0.341	−0.149
Rostral length	0.620	0.352	0.453	0.146
Orbitotemporal length	0.122	0.052	0.254	0.753
Maxillary toothrow length	0.497	−0.583	0.161	0.032
Labial palatal breadth at M^1	0.547	−0.457	0.428	−0.044
Diastema length	0.391	0.755	0.034	0.118
Postpalatal length	0.763	0.159	0.005	−0.247
Lingual palatal breadth at M^3	0.712	0.098	−0.245	−0.111
Braincase height	0.234	−0.496	−0.323	0.663
Breadth of M^1	−0.039	−0.469	0.758	−0.011
Breadth of incisors at tip	0.726	−0.160	0.023	−0.347
Width of zygomatic plate	0.507	−0.520	−0.126	−0.175
Eigenvalue	6.105	2.613	1.979	1.457
Percent variance explained	33.92	14.52	10.99	8.096

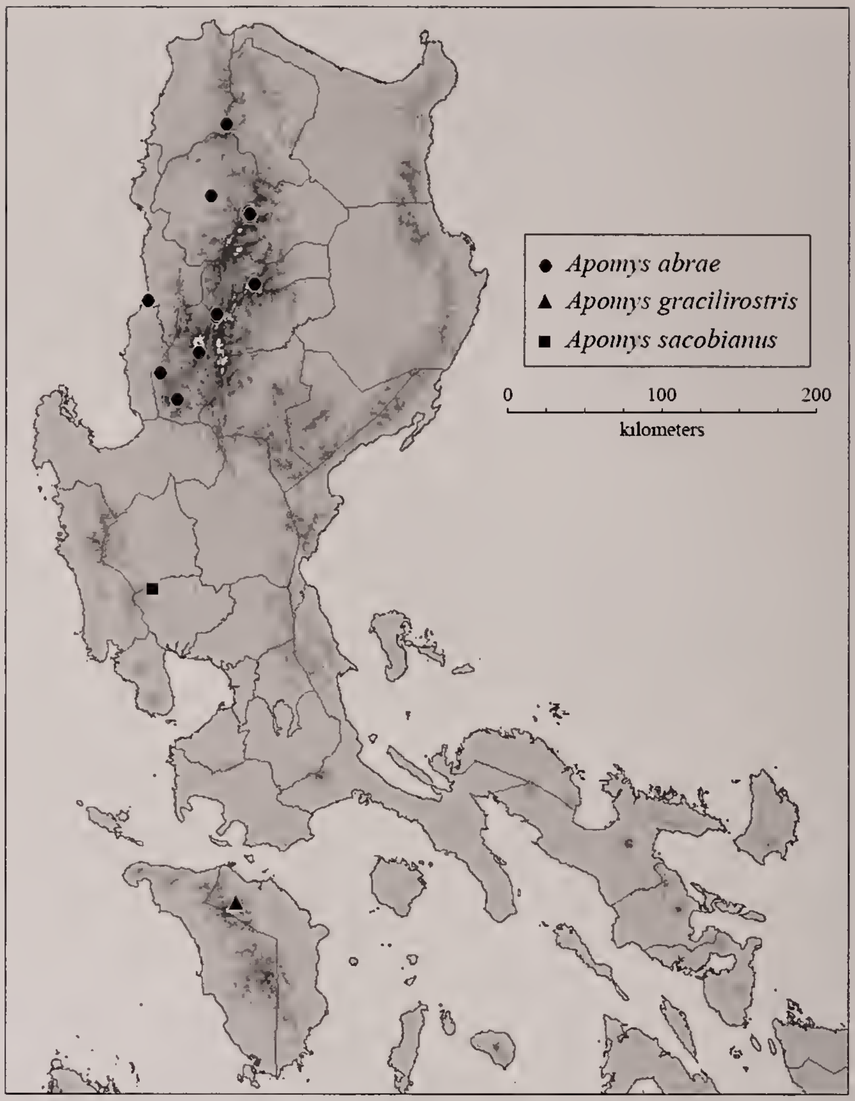


FIG. 18. Map showing the documented distribution of *Apomys abrae*, *A. gracilirostris*, and *A. sacobianus*. See respective species accounts for localities. Shading on land areas, in increasingly dark tones of gray: 0–500 m elevation; 501–1000 m; 1001–1500 m; 1501–2000 m; and white above 2000 m. Provincial boundaries are shown for reference.

field and preserved in ethanol before the specimen was preserved in formaldehyde. In the museum, the skull was removed and cleaned (see Methods). All parts are in good condition. This specimen will be permanently deposited at the NMP. Measurements in Table 3.

TYPE LOCALITY—Philippines: Luzon Island: Zambales Province: Palauig Munic.: Barangay Salasa: Mt. Tapulao peak, 2024 m; 15°28′54.8″N, 120°07′10.4″E (GPS reading).

PARATYPES (n = 34)—Luzon Island: Zambales Prov.: Palauig Munic.: Brgy. Salasa: Mt. Tapulao peak, 2024 m (FMNH 183494–183523, 183525–183528).

ETYMOLOGY—"brown" + "*orum,*" meaning "of the Browns," a plural noun used in the genitive. We name this species in recognition of the long-standing support for research on mammalian diversity by Barbara and Roger Brown, without which our studies of Philippine mammals would not have been possible.

DIAGNOSIS AND DESCRIPTION—A mouse with especially soft, richly colored pelage and a relatively short tail. It is the smallest species of *Megapomys* (e.g., BOL 32.4–34.9 mm, HBL 126–140 mm; Table 3). The dorsal pelage is soft, dense, and moderately long; it is a rich dark brown, sometimes with rusty-orange tints between the eye and pinna and below the pinna and along the lower margin of the dorsal pelage (Fig. 2B). The ventral pelage is dark gray at the base, with grayish-ochraceous tips. The transition between the dorsal and ventral pelage is gradual. Dark hairs extend from the lower forelimb onto the posterior third of the forepaws, and from the lower hind leg over about four-fifths of the dorsal surface of the hind foot. The hind feet are pale ventrally, with little or no pigment (Fig. 10H). The tail is proportionately short (82–90% of HBL) and sharply bicolored, with the dorsal surface dark grayish-brown and the ventral surface nearly white. The cranium (Fig. 24; Table 3) is small, with a relatively slender rostrum and zygomatic arches and a globose braincase. The incisive foramina are short (4.8–5.2 mm) and narrow. The maxillary molariform toothrow is short (6.4–6.8 mm), and the toothrow is narrow, as shown by the width of M^1 (1.63–1.79 mm). The maxillary toothrows diverge slightly posteriorly, and the palate is lightly pitted and perforated. The bulla has no perforation for a stapedial artery (the "abrae pattern"; Fig. 5A). The postpalatal region is unusually short (Table 3). The interparietal bone is of moderate anteroposterior width and is usually oval in shape. The mandible (Fig. 24C) is short and rather slender, with a long, pointed coronoid process, short angular process, and a shallowly concave margin between the condylar and angular processes.

COMPARISONS—*Apomys brownorum* differs from *A. datae* in being smaller in all respects, with little overlap in any measurement (Tables 2, 3). The tail is both absolutely (110–115 vs. 121–142 mm) and proportionately (70–88% of HBL vs. 88–103%) shorter. The pelage of *A. brownorum* (Fig. 2B) is darker than that of *A. datae* (Fig. 1B), both dorsally and ventrally. The hind foot is not as dark ventrally as that of *A. datae*, with only a small amount of pigment on most individuals. The foot and toes are broader than those of *A. datae* (Fig. 10B,H). The skin of the rhinarium and lips of *A. brownorum* is less dark. The skull of *Apomys brownorum* is more slender and gracile overall, and they are easily distinguished. The braincase of *A. brownorum* (Fig. 24) is slightly more elongated and globose, the interorbital region more constricted, and the rostrum proportionately shorter and more gracile; the upper incisors are thinner in both dimensions, the incisive foramina are usually narrower, both the

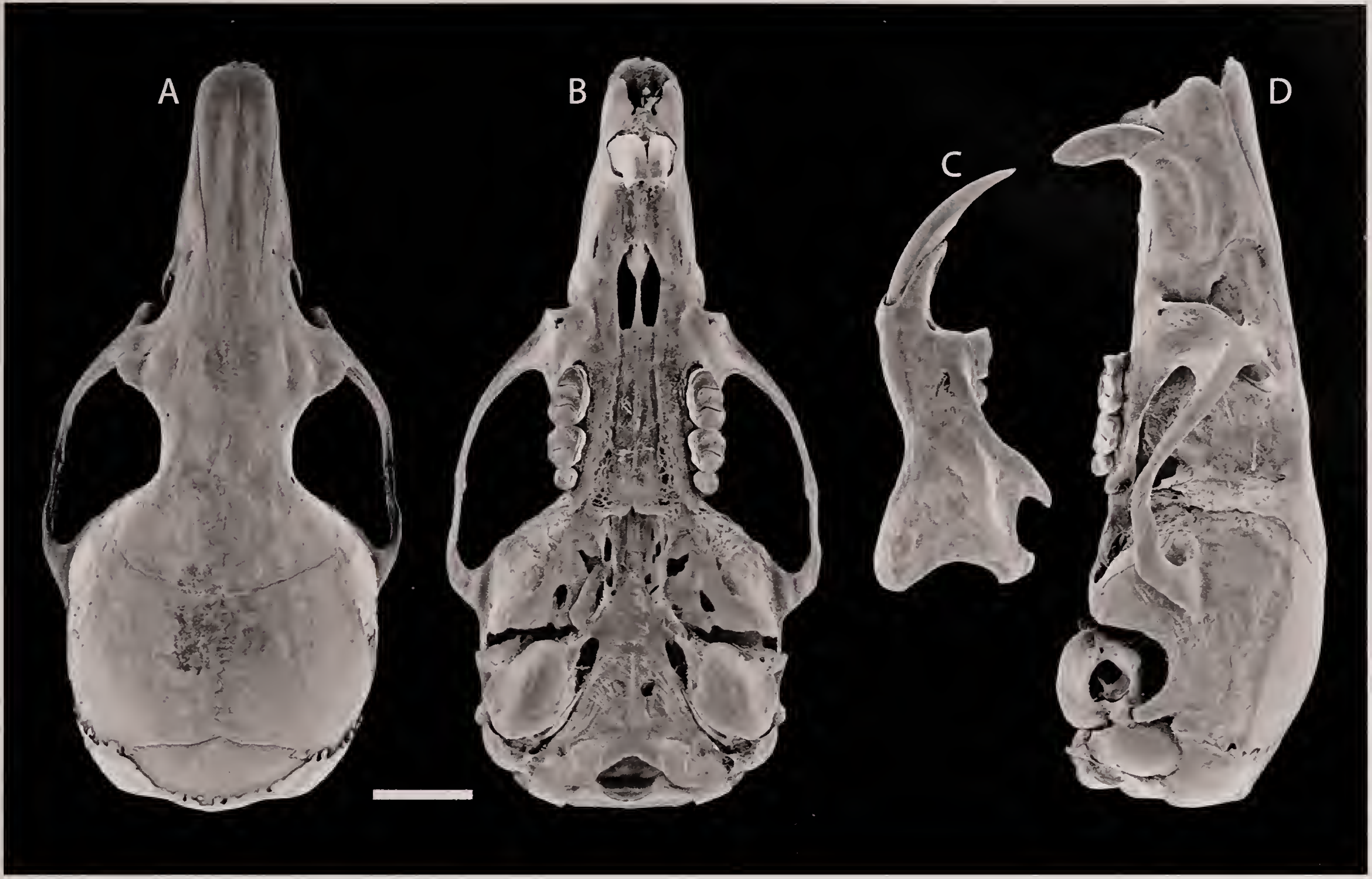


FIG. 19. Dorsal (**A**), ventral (**B**), and lateral (**D**) views of the cranium and lateral view of the mandible (**C**) of *Apomys gracilirostris* (NMP 3478); scale bar = 5 mm.

zygomatic plate and the palate are absolutely and proportionately narrower, and the postpalatal region is shorter. *Apomys brownorum* has the "abrae pattern" of basicranial circulation, with no stapedial foramen in the bullae (Fig. 5A). The interparietal bones are of similar shape. The mandible (Fig. 24C) is shorter and more slender than that of *A. datae*, with a more erect and sharply pointed coronoid process, and the posterior margin between the condylar and angular processes is slightly more concave.

Apomys brownorum and *A. banahao* sp. nov. are generally similar but also show consistent differences. Both species have long, soft, and dense pelage dorsally that is dark brown, but that of *A. brownorum* (Fig. 2B) is slightly paler and shorter. Both species have ventral fur that is dark gray at the base and quite pale near the tips, but *A. brownorum* is washed with pale ochraceous, whereas *A. banahao* sp. nov. (Fig. 1D) is washed with ashy gray. The tail in both species is sharply dorsoventrally bicolored; neither possesses a white tip. The tail of *A. brownorum* is usually shorter than that of *A. banahao* sp. nov. both absolutely (110–115 vs. 111–133 mm) and relative to the length of head and body (70–88% vs. 87–103%; Fig. 25A). Both species have dark hairs present over much of the dorsal surface of the hind foot, but the ventral surface in *A. brownorum* is much less heavily pigmented than that of *A. banahao*, and is slightly broader (Fig. 10C,H).

The skull of *A. brownorum* is similar to that of *A. banahao* sp. nov. but is smaller overall. The braincase is slightly more elongate and globose (vs. somewhat more rectangular), the rostrum is relatively more elongate and gracile, the incisive foramina are less broad, the zygomatic plate is narrower and the orbitotemporal fossa length is usually less (Fig. 25B), and a plot of breadth of M^1 vs. labial breadth of palate at M^1 shows almost no overlap (Fig. 25C); this combination of mensural characters separates all individuals. The palate of *A. banahao* sp. nov. is more heavily pitted and fenestrated. These species share the "abrae pattern" of carotid circulation, lacking a stapedial foramen in the bullae (Fig. 5A). The interparietals are similar in shape. The mandible of *A. banahao* sp. nov. is similar to that of *A. brownorum*, but the coronoid process is shorter, thinner, and directed more posteriorly, and the posterior margin between the condylar and angular processes is shallower.

A PCA of 18 craniodental measurements showed substantial differences between these two species (Fig. 26; Table 8). The first component, which accounted for 49% of the total variance, loaded strongly on all measurements, indicating that it is an indicator of size and robustness. The second component, which accounted for 11% of the total variance, was strongly dominated by high loadings on rostral and diastema length (Table 8). Subsequent components had eigenvalues of less than 2.0. Individuals of *A. brownorum* had low scores on the first component, whereas most *A. banahao* sp. nov. had higher scores, reflecting the generally greater size and robustness of the latter species. Overlap was great on the second component, although some *A. brownorum* scored low on the component, indicating their proportionately

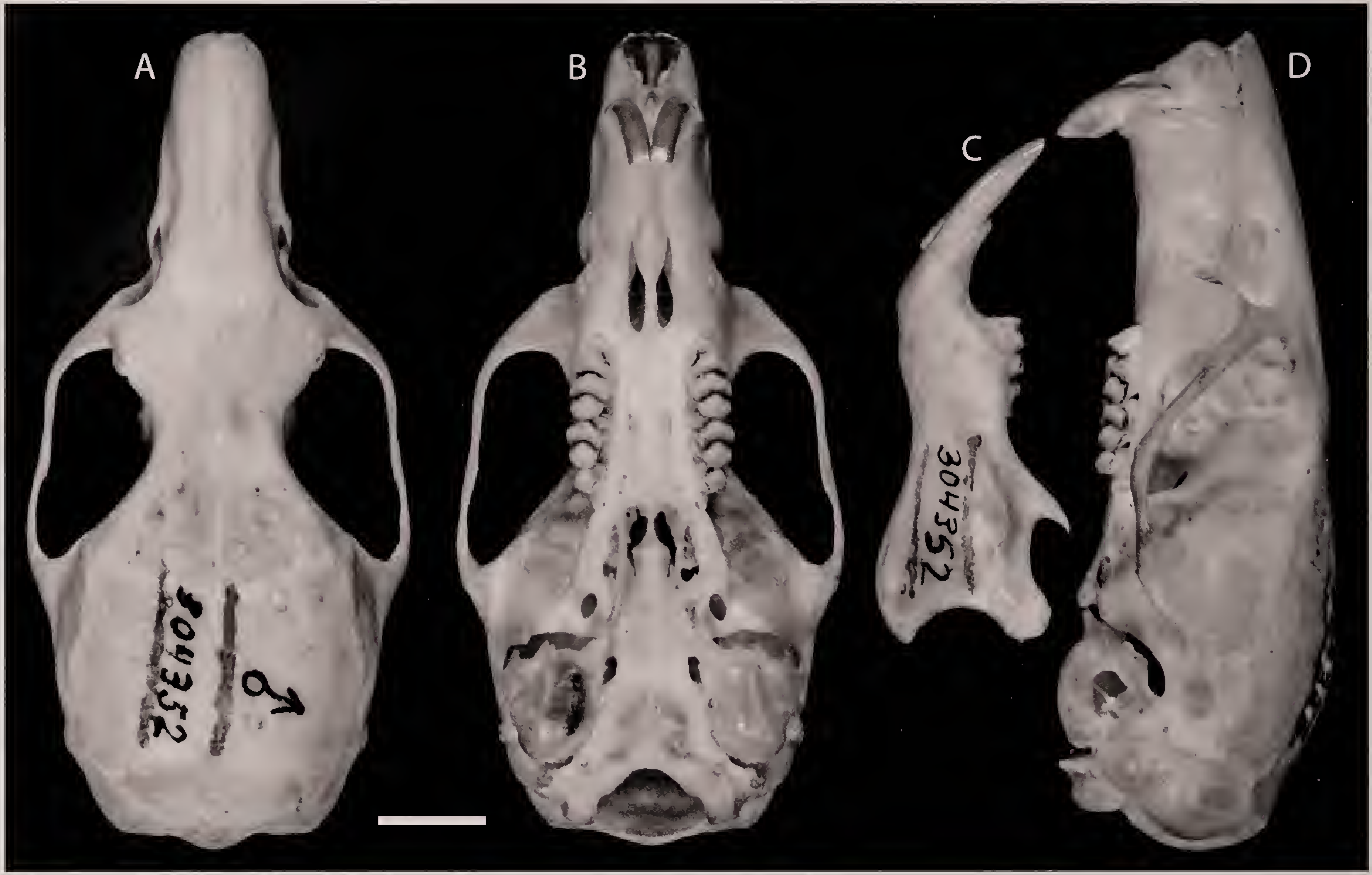


FIG. 20. Dorsal (**A**), ventral (**B**), and lateral (**D**) views of the cranium and lateral view of the mandible (**C**) of *Apomys sacobianus* (USNM 304352, holotype); scale bar = 5 mm.

long rostrum and diastema. Given the strong and consistent morphological and genetic differences that distinguish these species, we consider them to be distinct species.

Apomys brownorum differs in many respects from *A. zambalensis* sp. nov., which occurs on the same mountain (Mt. Tapulao) at lower elevations. Externally, there is little overlap in head and body length and no overlap in a plot of length of tail and hind foot (Fig. 27A), and most individuals of *A. zambalensis* sp. nov. are heavier (Tables 3, 15). The pelage of *A. brownorum* (Fig. 2B) is much darker dorsally and ventrally than *A. zambalensis* sp. nov. (Fig. 2A), which is a rich orange-brown dorsally and has a very pale ochraceous wash ventrally. The obvious morphological differences and genetic distance between them mark these as clearly distinct species.

Apomys brownorum and *A. zambalensis* sp. nov. are easily distinguished cranially, and there is no overlap in a plot of PC1 and PC2 from the PCA of cranial measurements (Fig. 6A). *Apomys brownorum* is consistently smaller in virtually all measurements (Tables 3, 15); the skull of *A. brownorum* is generally more slender, with a more globose braincase and a more delicate rostrum (vs. squarish braincase with a sturdy rostrum; Figs. 24, 46). The upper incisors are narrower and also less deep, and the incisive foramina are narrower. The palate is shorter and narrower, the molar toothrow is shorter (Fig. 27B), the zygomatic plate is narrower, and the lingual breadth at M^3 is usually less (Fig. 27C). *Apomys brownorum* lacks a stapedial foramen in the bullae (Fig. 5A); the foramen is present in *A. zambalensis* sp. nov. (Fig. 5B). The interparietal bone of *A. brownorum* is of moderate anteroposterior width; that of *A. zambalensis* sp. nov. is much wider. The mandible of *A. zambalensis* sp. nov. is longer and more robust overall, with a shorter, wider, more posteriorly inclined coronoid process and a broader, longer angular process. All individuals are easily distinguished by this combination of characters.

DISTRIBUTION—*Apomys brownorum* is currently known only from mossy forest at a single locality near the peak of Mt. Tapulao at ca. 2024 m elevation (Figs. 3, 14). No specimens were taken at 1690 m in 391 trap-nights that yielded 50 captures of *A. zambalensis* sp. nov. or at lower elevations where *A. zambalensis* sp. nov. were equally common. We have no data from 1690 to 2024 m, so we can infer only that the lower elevational limit for the species falls somewhere within this range, perhaps at ca. 1800 m, where there is a transition from montane to mossy forest (Balete et al., 2009). Similar habitat might occur on the other high peaks of the Zambales Mountains, and this species should be sought there, especially above about 1800 m. The Zambales Mountains are isolated from other highland areas by a broad lowland plain; the Central Cordillera, which has two species of *Megapomys* (*A. abrae* and *A. datae*), is the nearest mountain range, so we doubt that *A. brownorum* occurs outside of the Zambales Mountains.

Apomys (*Megapomys*) *banahao* sp. nov.

HOLOTYPE—FMNH 178501, adult male collected on 09 May 2004 by Eric A. Rickart, field number EAR 5279. A sample of

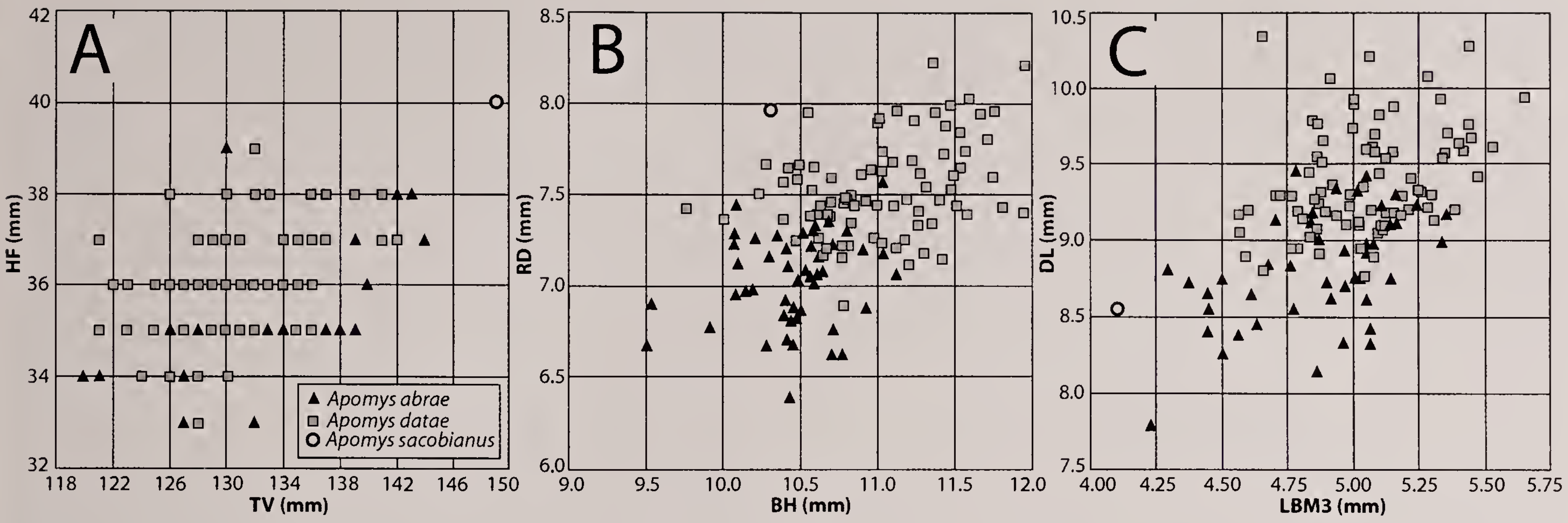


FIG. 21. Bivariate plots of measurements comparing *Apomys abrae*, *A. datae*, and *A. sacobianus*. (**A**) Length of tail vertebrae (TV) and length of hind foot (HF). (**B**) Braincase height (BH) and rostral depth (RD). (**C**) Lingual breadth of palate at M^3 (LBM^3) and diastema length (DL).

muscle tissue was removed from the thigh in the field and preserved in ethanol before preserving the specimen in formaldehyde. In the museum, the skull was removed and cleaned (see Methods). All parts are in good condition. This specimen will be permanently deposited at the NMP. Measurements are in Table 9.

TYPE LOCALITY—Philippines: Luzon Island: Quezon Province: Mt. Banahaw: Barangay Lalo, 1465 m; 14.06635°N, 121.50855°E (from GPS).

PARATYPES (n = 137)—Luzon Island: Quezon Prov.: Tayabas Munic.: Brgy. Lalo: Mt. Banahaw, 1465 m (FMNH 178358, 178359, 178397, 178430–178510, 179450–179494, 179496–178500, 179502, 179507, 179508); Tayabas Munic.: Brgy. Lalo: Mt. Banahaw, 1750 m (FMNH 178511–178544, 179503–179506, 179509–179517).

ETYMOLOGY—From the traditional Tagalog spelling of the name of the mountain (Banahao) where this species occurs, used as a noun in apposition.

DIAGNOSIS AND DESCRIPTION—A small species of the subgenus *Megapomys* (HBL 125–146 mm, BOL 33.10–35.25 mm) with a fairly short tail (86–103% of HBL). The dorsal pelage is soft, dense, and moderately long; it is dark brown, slightly paler laterally, with slight rusty tints (Fig. 1D). The ventral pelage is dark gray at the base and white washed with pale ashy-gray at the tips. The transition between the dorsal and ventral pelage is usually fairly abrupt. The ears are darkly pigmented. Dark brown fur covers the lower forelimb and about half of the posterior portion of the forepaws and is present as a dark brown area of variable size on about the center of the dorsal surface of the hind foot, with white fur both anterior and posterior. The hind feet are pigmented ventrally (Fig. 10C). The tail is sharply bicolored, with the dorsal surface dark grayish-brown and the ventral surface nearly white.

The cranium of *A. banahao* (Fig. 28; Table 9) is small, with a moderately long, slender rostrum. The zygomatic plate is wide (2.94–3.52 mm) relative to the length of the cranium. The incisive foramina are short (4.7–5.5 mm) and moderate in width. The maxillary molariform toothrow is moderately short (6.5–7.1 mm), and the toothrow is of moderate width, as shown by the width of M^1 (1.77–2.05 mm). The posterior portion of the palate is more extensively pitted and perforated than any species except *A. magnus* sp. nov., which is similar in this character. There is no perforation of the bulla for a stapedial artery (the "abrae pattern"; Fig. 5A). The mandible (Fig. 28C) is relatively small and slender, with a short, sharply pointed coronoid process, sturdy angular process, and shallow posterior margin between the condylar and angular processes.

The karyotype of *A. banahao*, based on three males from Mt. Banahaw (FMNH 178481, 178482, 178524), is 2n = 48, FN ≥ 54 (Fig. 8D). The autosomal complement includes two pairs of small metacentric or submetacentric chromosomes and 21 pairs of telocentric or subtelocentric chromosomes. The X chromosome is large and submetacentric, and the Y is very small and acrocentric.

COMPARISONS—*Apomys banahao* (Fig. 1D) is easily distinguished from *A. datae* (Fig. 1B). It is smaller in nearly all measurements (Tables 2, 9), but with some overlap. Its dorsal pelage is softer and denser and is slightly darker and less rusty-red in tone. The ears of *A. banahao* are more darkly pigmented. The ventral pelage is paler, and there are fewer dark hairs on the dorsal surface of the hind feet. The rostrum is shorter and less robust, the braincase is more globose and less squarish, the interorbital breadth is less, the palate is narrower, and the bullae lack a foramen for the stapedial artery ("abrae type"; Fig. 5A), which is conspicuous in *A. datae* (Fig. 5B). The interparietals are similar in shape. The mandible of *A. datae* is much larger and proportionately more robust, with a longer, wider coronoid process and broader, longer angular process.

Apomys banahao is equally easily distinguished from *A. magnus* sp. nov., with which it occurs syntopically at middle elevations on Mt. Banahaw. It is smaller on average in virtually all measurements, although with some overlap (Tables 9, 12). A comparison of length of head and body and length of tail distinguishes most individuals (Fig. 29A). Its dorsal pelage is longer and softer (Fig. 1D) and is less rusty than *A. magnus* sp. nov. (Fig. 1E), and it lacks the conspicuous black tips on the dorsal guard hairs of *A. magnus* sp. nov. Its fore- and hind feet have black hairs on the dorsal surface, whereas those of *A. magnus* are nearly entirely white. The ventral pelage of *A. banahao* is dark gray at the base, with pale gray tips; that of *A. magnus* sp. nov. is pale gray at the base with white tips. Its skull is much smaller and far more gracile, usually with a narrower interorbital region (Fig. 29B). The rostrum of *A. banahao* is shorter and less robust, and the

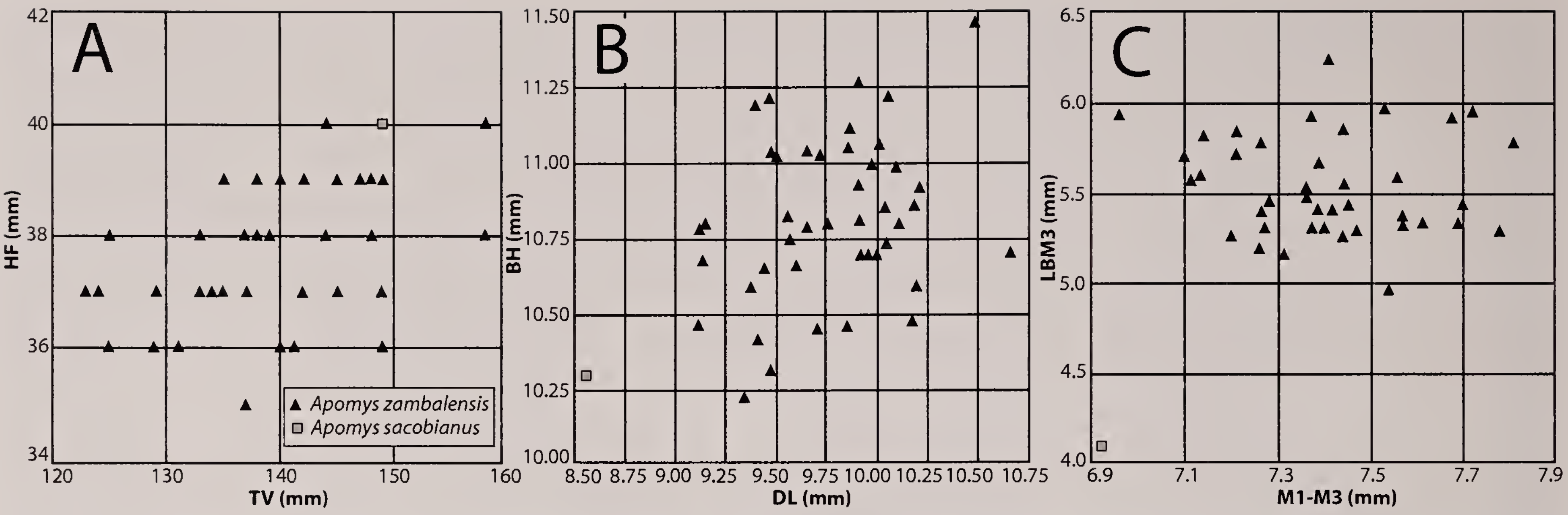


FIG. 22. Bivariate plots of measurements comparing *Apomys sacobianus* and *A. zambalensis* sp. nov. (**A**) Length of tail vertebrae (TV) and length of hind foot (HF). (**B**) Diastema length (DL) and braincase height (BH). (**C**) Length of maxillary molariform toothrow (M^1–M^3) and lingual breadth of palate at M^3 (LBM^3).

braincase is much less square (more globose) than that of *A. magnus* sp. nov. The incisive foramina are less broad, and the zygomatic plate is narrower. The maxillary toothrow is both shorter and narrower, and the palate is narrower (Fig. 29C). The bullae lack a foramen for the stapedial artery (the "*abrae* pattern"; Fig. 5A), which is conspicuous in *A. magnus* sp. nov. (Fig. 5B). The interparietal bone of *A. banahao* is moderate in anteroposterior width; that of *A. magnus* sp. nov. is much wider. The mandible of *A. magnus* sp. nov. is larger and more robust, with a less slender coronoid process and a broader angular process. The combination of clear morphological and genetic differences strongly supports the recognition of these as distinct species.

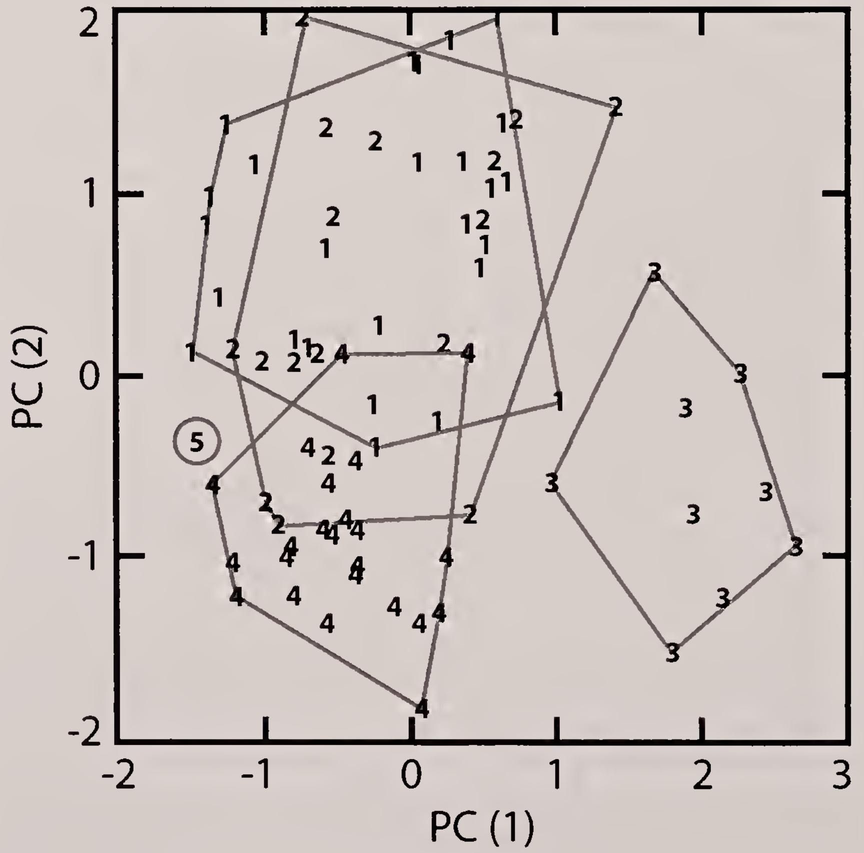


FIG. 23. Results of the principal components analysis of *Apomys aurorae* sp. nov., *A. magnus* sp. nov., *A. sacobianus*, and *A. zambalensis* sp. nov. (see text and Table 7) based on specimens included in Tables 3, 12, and 15. 1 = *A. zambalensis* from Mt. Natib, Bataan Province; 2 = *A. zambalensis* from Mt. Tapulao, Zambales Province; 3 = *A. magnus* from Quezon Province; 4 = *A. aurorae* from Aurora Province; 5 = *A. sacobianus* from Pampanga Province.

Apomys banahao is generally similar to its sister-species, *A. brownorum*, but differs in having pelage that is paler and shorter, ventral fur that is washed with ashy gray (rather than a pale ochraceous wash), a relatively shorter tail, a larger cranium overall, a narrower M^1 and palate, and usually narrower zygomatic plate and foramina (for details, see above). A PCA of craniodental measurements (Fig. 26; Table 8) reflected these differences, as discussed above.

DISTRIBUTION—*Apomys banahao* is known from 1465 to 1750 m on Mt. Banahaw (Figs. 3, 14, 15) and probably occurs from about 1400 m up to the peak at 2177 m. It should be sought on the adjacent mountain, Mt. San Cristobal, which rises to 1470 m. Because Mts. Banahaw and San Cristobal are isolated in a broad, low-elevation plain, we predict that this species will not be found in any other area. If that is the case, then its distribution is among the smallest of *Megapomys* species.

Apomys (*Megapomys*) *minganensis* sp. nov.

HOLOTYPE—FMNH 190949, adult male collected on 05 June 2006 by Mariano Roy M. Duya, field number MRMD 416. A sample of muscle tissue was removed from the thigh in the field and preserved in ethanol before preserving the specimen in formaldehyde. In the museum, the skull was removed and cleaned (see Methods). All parts are in good condition. This specimen will be permanently deposited at the NMP. Measurements appear in Table 9.

TYPE LOCALITY—Philippines: Luzon: Aurora Province: Dingalan Munic.: 1.5 km S, 0.5 km W Mingan peak, 1681 m elevation, 15.46802°N, 121.40039°E (GPS reading).

PARATYPES (n = 97)—Luzon Island: Aurora Prov.: Dingalan Munic.: 1.7 km S, 1.3 km W Mingan Peak, 1540 m (FMNH 190941–190946, 190954, 190955); Dingalan Munic.: 1.8 km S, 1.0 km W Mingan Peak, 1677 m (FMNH 190774–190777, 190833–190845, 190847, 190848, 190936–190940); Dingalan Munic.: 1.5 km S, 0.5 km W Mingan Peak, 1681 m (FMNH 190787–190793, 190867–190886, 190947, 190948, 190950–190952, 190956–190960); Dingalan Munic.: 0.9 km S, 0.3 km W Mingan Peak, 1785 m (FMNH 190778–190786, 190849–190866, 191065).

ETYMOLOGY—An adjective based on the name of the mountain range (Mingan Mountains) where this species occurs.

TABLE 7. Character loadings, eigenvalues, and percent variance explained on the first four components of a principal components analysis of log-transformed measurements of adult *Apomys aurorae*, *A. magnus*, *A. sacobianus*, and *A. zambalensis* (see Fig. 23 and Methods).

Variable	Principal component			
	1	2	3	4
Basioccipital length	0.894	0.309	0.116	0.126
Interorbital breadth	0.570	−0.427	−0.271	−0.245
Zygomatic breadth	0.837	−0.073	−0.102	−0.017
Mastoid breadth	0.799	−0.188	−0.020	−0.043
Nasal length	0.813	0.156	0.004	0.025
Incisive foramen length	0.515	0.123	−0.013	0.449
Rostral depth	0.721	0.289	0.057	0.098
Rostral length	0.756	0.102	−0.302	0.115
Orbitotemporal length	0.735	−0.214	0.107	0.185
Maxillary toothrow length	0.727	−0.237	0.330	−0.054
Labial palatal breadth at M^1	0.753	−0.420	0.038	−0.143
Diastema length	0.651	0.531	−0.291	0.091
Postpalatal length	0.573	0.615	0.301	0.031
Lingual palatal breadth at M^3	0.540	0.155	−0.479	−0.453
Braincase height	0.564	−0.144	−0.144	−0.283
Breadth of M^1	0.482	−0.743	0.270	0.043
Breadth of incisors at tip	0.624	0.072	0.409	−0.117
Width of zygomatic plate	0.086	−0.431	−0.380	0.657
Eigenvalue	8.109	2.179	1.124	1.101
Percent variance explained	45.05	12.116	6.25	6.12

DIAGNOSIS AND DESCRIPTION—A fairly small species of *Megapomys* (HBL 128–145 mm, BOL 33.2–35.0 mm; Table 9), with a tail about 94% (range 87–101%) of HBL. The dorsal pelage is dark brown with rusty-orange tips on the hairs, lying over dark gray underfur (Fig. 2E). The ventral pelage is dark gray at the base, with paler tips that usually have an ochraceous wash. On live or fresh specimens, the eyes are noticeably small. The tail is dark brown dorsally, always with some dark hairs and pigment in the scales ventrally; nearly all individuals have a small white tip, 1–4 mm long, on the tail. The dorsal surface of the hind feet is dark brown, with dark brown hairs reaching fully onto the toes; the ventral surface is lightly to heavily pigmented, except the pads, which are usually less darkly pigmented (Fig. 10F). The hallux is long, reaching to or nearly to the top of the adjacent plantar pad (Fig. 10F). The forefeet are almost entirely covered by dark fur that extends down onto the foot from the forearm. The pigmented area at the posterior tip of the scrotum of adult males is very dark brown.

The skull of *A. minganensis* (Fig. 30) is of average overall size in the subgenus *Megapomys*, with a BOL of 33.2–35.0 mm. In general configuration, the skull is similar to those of *A. aurorae* sp. nov. and *A. sierrae* sp. nov. in having a fairly globose braincase, moderately gracile rostrum, broad incisive foramina, lightly pitted palate, and the "datae pattern" of carotid circulation (Fig. 5B). The rostrum of *A. minganensis* is relatively short and narrow, and the orbitotemporal and postpalatal regions are short. The maxillary toothrow of *A. minganensis* is unusually short, the molars are narrow, and the molar toothrows are nearly parallel. The interparietal is variable in shape but usually is somewhat narrow in anteroposterior width. The mandible is short and slender, with a short coronoid process and relatively narrow angular process.

COMPARISONS—Compared with the sympatric *A. aurorae* sp. nov., *A. minganensis* differs externally in many respects. *Apomys minganensis* has dark dorsal fur with rusty tips and dark gray underfur (Fig. 2E), rather than rich rusty-brown fur with medium gray underfur (Fig. 2F), and is darker ventrally, having fur that is dark gray at the base (rather than medium to pale gray), with tips with an ochraceous wash (rather than white or nearly white with a pale ochraceous wash). The hind feet of *A. minganensis* are covered by dark hairs dorsally, whereas those of *A. aurorae* sp. nov. are usually white or have scattered dark hairs that do not reach the base of the toes (i.e., the hair at the base of the toes is white). The hind feet of *A. minganensis* are typically shorter and broader than those of *A. aurorae* sp. nov., and the hallux of *A. aurorae* sp. nov. is shorter, typically reaching only the base or the middle of the adjacent plantar pad (Fig. 10G). The forefeet of *A. minganensis* have dark fur over the entire dorsal surface, but those of *A. aurorae* sp. nov. are usually white, sometimes with dark hairs over a central strip of the forefoot. The tail of *A. minganensis* is always dark dorsally and usually has substantial amounts of pigment and dark hair ventrally, whereas that of *A. aurorae* sp. nov. is dark to medium brown dorsally and either pure white or white with only some scattered dark hairs and bits of dark pigment ventrally. *Apomys minganensis* nearly always has a tiny white tip on the tail (over 95%), whereas *A. aurorae* sp. nov. rarely has such a tip (less than 3%). The tail of *A. aurorae* sp. nov. averages longer than that of *A. minganensis*, and *A. aurorae* n. sp. also averages greater in HBL, but there is considerable overlap in both of these measurements (Fig. 31A).

The skull of *A. minganensis* is also easily distinguished from that of *A. aurorae* sp. nov. There is no overlap in rostral depth, orbital length, or length of the maxillary toothrow (Tables 9, 15; Fig. 31B,C); the M^1 of *A. minganensis* is narrower; and there is little overlap in lingual breadth of the palate at M^3 (Fig. 31C) or in postpalatal length. Overall, the skull of *A. minganensis* is slightly smaller and less elongate than that of *A. aurorae* sp. nov. The carotid circulation pattern is the same in these two species. The interparietal of *A. minganensis* is usually narrower than that of *A. aurorae* sp. nov. The mandible of *A. aurorae* sp. nov. is larger and more robust than that of *A. minganensis*, with a longer and more slender coronoid process and broader angular process.

Apomys minganensis is closely related to *A. sierrae* sp. nov. and also occurs nearby. These two species are easily distinguished. *Apomys minganensis* has longer, denser dorsal fur that is dark brown rather than the rusty reddish-brown of nearby populations of *A. sierrae* sp. nov. (Fig. 2E,C). The ventral fur of *A. minganensis* is usually dark gray at the base and pale gray with an ochraceous wash at the tips, whereas *A. sierrae* sp. nov. has ventral fur that is medium to pale gray at the base and either white or white washed with ochraceous at the tips. The tail of *A. minganensis* is much darker dorsally, always with scattered dark hairs and pigment ventrally; that of *A. sierrae* sp. nov. is less dark dorsally and usually unpigmented ventrally. Additionally, the tip (1–4 mm) of the tail is white dorsally and ventrally in about 95% of *A. minganensis*, whereas that of *A. sierrae* sp. nov. virtually always retains the usual dorsal and ventral color. The dorsal surface of the hind foot of *A. minganensis* is covered by dark hair, whereas that of *A. sierrae* sp. nov. has only a few scattered dark hairs among the predominantly white hair. The hallux of *A. sierrae* sp. nov. is short, reaching only to about the base of the adjacent interdigital plantar pad, whereas that of *A. minganensis* is longer, reaching to the middle or top of the adjacent pad. External measurements of these two species are generally

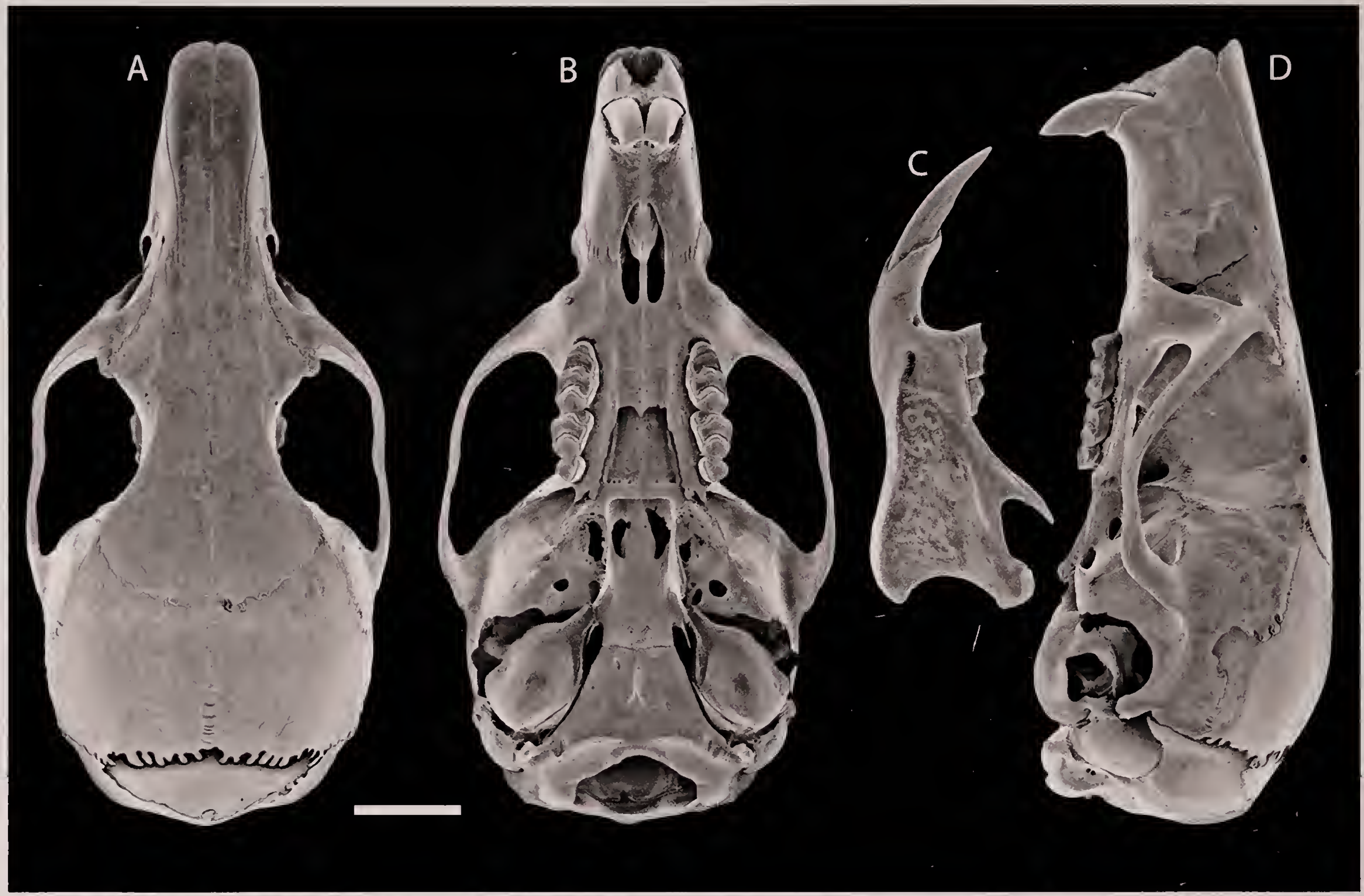


FIG. 24. Dorsal (**A**), ventral (**B**), and lateral (**D**) views of the cranium and lateral view of the mandible (**C**) of *Apomys brownorum* sp. nov. (FMNH 183524, holotype); scale bar = 5 mm.

similar and overlapping (Tables 9, 11, 12), but *A. sierrae* sp. nov. averages larger in most respects (e.g., ear and hind foot length; Fig. 32A).

The skull of *A. minganensis* (Fig. 30) is similar to that of *A. sierrae* sp. nov. (Fig. 34), but a number of unambiguous differences are apparent, and there is no overlap in the PC1 and PC2 of cranial measurements in the PCA that includes all *Megapomys* (Fig. 6A). Overall, the skull of *A. minganensis* is a bit shorter and more compact than that of *A. sierrae* sp. nov., with a distinctly less robust rostrum (no overlap in rostral depth), a shorter toothrow with narrower molars, and a palate that is usually narrower (Fig. 32B,C). The maxillary toothrows of *A. minganensis* are nearly parallel, whereas those of *A. sierrae* sp. nov. diverge posteriorly, and the palate of *A. sierrae* sp. nov. is more heavily pitted and perforated. In *A. sierrae* sp. nov., the foramen in the bulla for the stapedial artery is absent (the "abrae pattern"; Fig. 5A), whereas in *A. minganensis,* it is always present (the "datae pattern"; Fig 5B). The interparietal

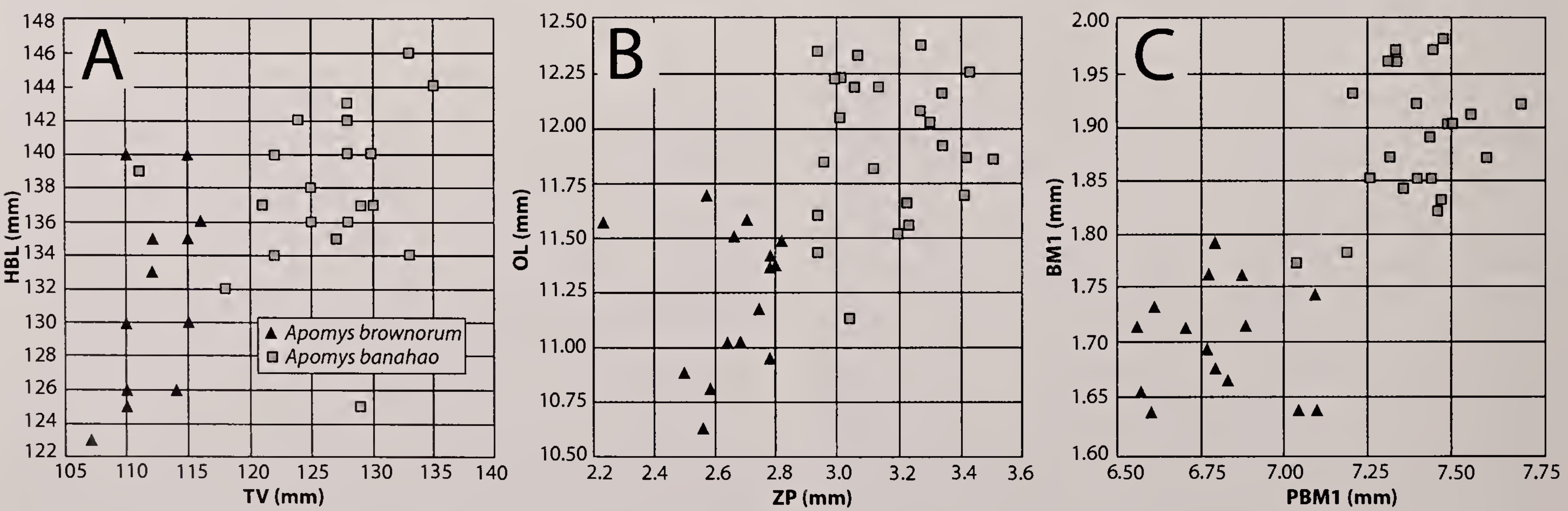


FIG. 25. Bivariate plots of measurements comparing *Apomys brownorum* and *A. banahao* spp. nov. (**A**) Length of tail vertebrae (TV) and length of head and body (HBL). (**B**) Zygomatic plate width (ZP) and orbitotemporal length (OL). (**C**) Labial palatal breadth at M^1 (PBM^1) and breadth of M^1 (BM^1).

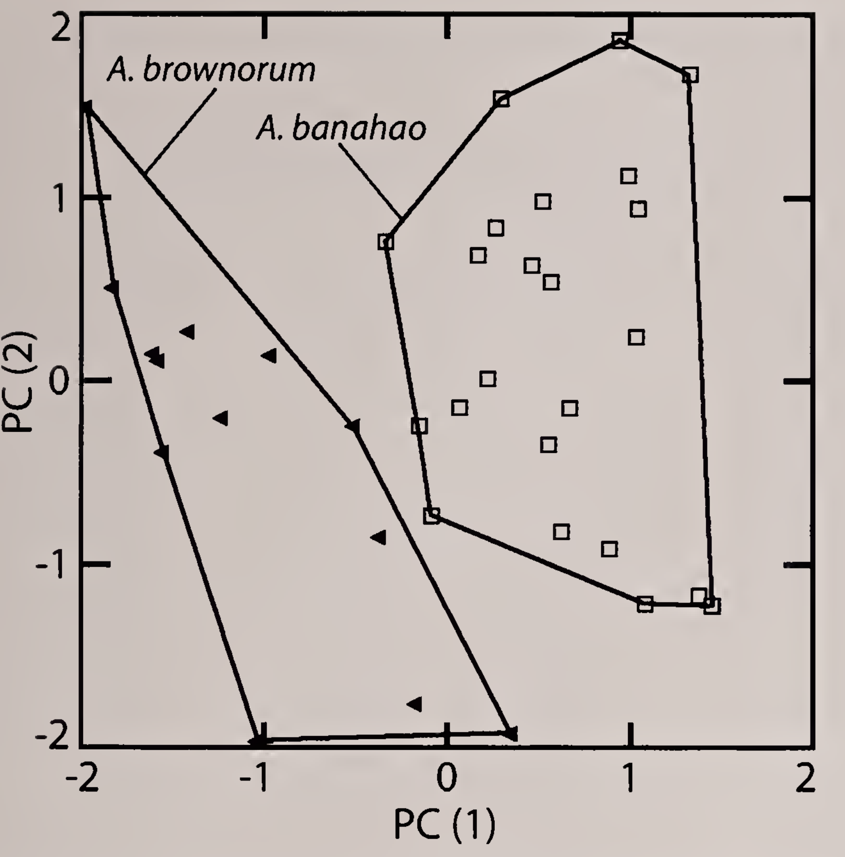


FIG. 26. Results of the principal components analysis of *Apomys brownorum* and *A. banahao* spp. nov. (see text and Table 8) based on specimens in Tables 3 and 9.

TABLE 8. Character loadings, eigenvalues, and percent variance explained on the first four components of a principal components analysis of log-transformed measurements of adult *Apomys banahao* and *A. brownorum* (see Fig. 26 and Methods).

Variable	Principal component 1	2	3	4
Basioccipital length	0.897	−0.334	−0.036	−0.004
Interorbital breadth	0.740	0.434	0.282	0.090
Zygomatic breadth	0.901	0.179	0.164	0.104
Mastoid breadth	0.668	0.274	0.447	−0.281
Nasal length	0.635	−0.433	−0.029	−0.303
Incisive foramen length	0.313	0.073	−0.659	−0.019
Rostral depth	0.906	0.114	0.162	0.059
Rostral length	0.434	−0.699	0.065	−0.187
Orbitotemporal length	0.761	0.080	−0.155	−0.331
Maxillary toothrow length	0.634	−0.149	−0.423	−0.221
Labial palatal breadth at M^1	0.880	0.278	−0.217	0.171
Diastema length	0.445	−0.638	0.255	0.278
Postpalatal length	0.845	−0.344	−0.088	0.013
Lingual palatal breadth at M^3	0.615	−0.030	0.229	0.613
Braincase height	0.463	0.292	0.517	−0.414
Breadth of M^1	0.679	0.399	−0.480	−0.001
Breadth of incisors at tip	0.649	−0.035	0.195	0.046
Width of zygomatic plate	0.804	0.106	−0.267	0.186
Eigenvalue	8.904	1.991	1.754	1.077
Percent variance explained	49.47	11.06	9.75	5.99

of *A. minganensis* is usually anteroposteriorly narrower than that of *A. sierrae* sp. nov. The mandibles are similar, but that of *A. minganensis* is a bit more robust, with a more deeply concave posterior margin between the condylar and angular processes.

To further assess the distinctiveness of *A. minganensis* relative to *A. aurorae* sp. nov. and *A. sierrae* sp. nov., we conducted a PCA of 18 craniodental measurements of our samples of all three species (Tables 9, 11, 12, 15). The first component, which accounted for 40% of the total variance, loaded strongly on nearly all measurements, with rostral length, diastema length, and height of braincase loading least strongly (Table 10). The second component, which accounted for 15% of the variance, loaded most strongly (and positively) on rostral and diastema length and (negatively) on length of the molar toothrow and breadth of M^1. PC3 and PC4 had eigenvalues of less than 1.5. A plot of the first two components (Fig. 33) showed *A. minganensis* falling outside of the polygon of *A. sierrae* sp. nov. and far from that of *A. aurorae* sp. nov. Individuals of *A. minganensis* scored low on PC1, reflecting its small size relative to the other two species, although there was slight overlap at the margins of the polygons. On PC2, *A. minganensis* scored high, reflecting its long rostrum and diastema and short molar toothrow and narrow M^1. *Apomys aurorae* sp. nov. scored low on PC2, reflecting its typically shorter rostrum and diastema and longer molar toothrow and wider M^1, although these two species showed some overlap on this component. Individuals of *A. sierrae* sp. nov. varied greatly on PC2, overlapping extensively with *A. minganensis*, but most individuals scored lower than those of *A. minganensis*. We conclude that *A. minganensis* differs consistently from these two closely related species. Additional comparisons between *A. aurorae* sp. nov. and *A. sierrae* sp. nov., which overlap extensively on these two components, are made below.

DISTRIBUTION—We captured *A. minganensis* along our transect on the Mingan Mountains from 1540 to 1785 m

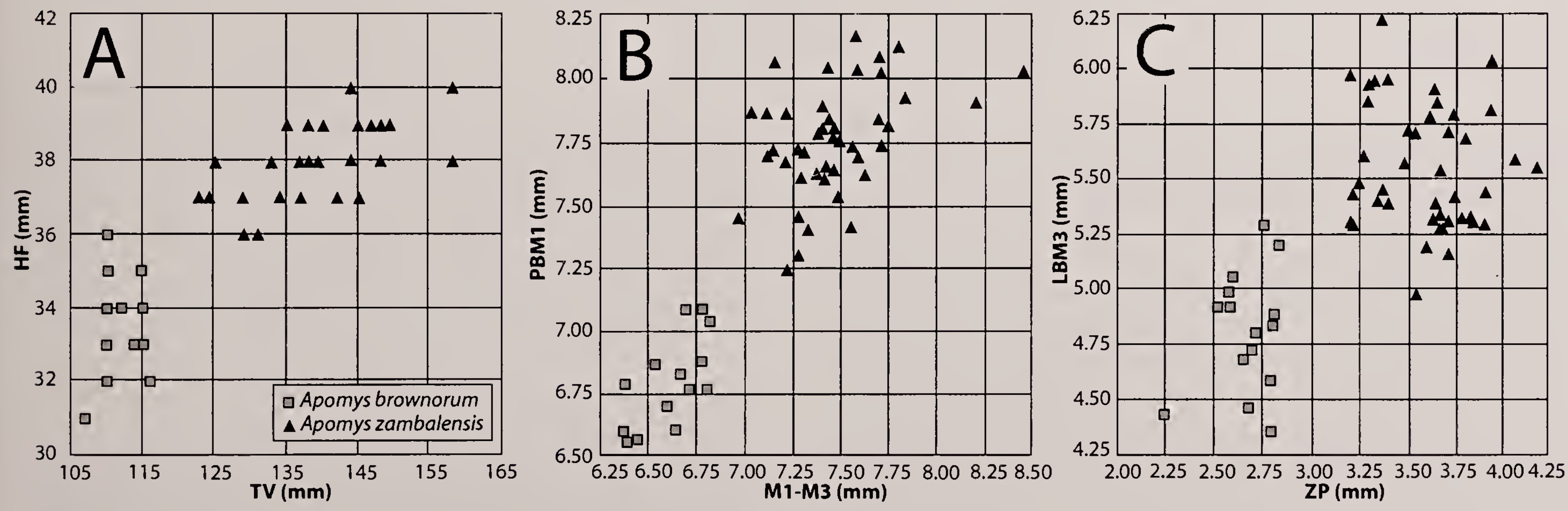


FIG. 27. Bivariate plots of measurements comparing *Apomys brownorum* and *A. zambalensis* spp. nov. (**A**) Length of tail vertebrae (TV) and length of hind foot (HF). (**B**) Length of maxillary molariform toothrow (M^1–M^3) and labial palatal breadth at M^1 (PBM^1). (**C**) Zygomatic plate width (ZP) and lingual breadth of palate at M^3 (LBM^3).

TABLE 9. Cranial and external measurements (mean ± 1 S.D. and range) of *Apomys banahao*, *A. minganensis*, and *A. sierrae* (part).

	Apomys banahao			*Apomys minganensis*		
	Mt. Banahaw, 1465–1750 m, Quezon Prov.			**Mingan Mtns., 1540–1785 m, Aurora Prov.**		
Measurement	**M-holotype FMNH 178501**	**M (n = 13)**	**F (n = 11)**	**M-holotype FMNH 190949**	**M (n = 9)**	**F (n = 10)**
Basioccipital length	34.23 —	34.43 ± 0.61 (12) 33.34–35.39	34.13 ± 0.74 33.10–35.25	34.82 —	34.06 ± 0.47 33.42–34.82	34.02 ± 0.55 33.16–34.97
Interorbital breadth	5.96 —	5.98 ± 0.28 (12) 5.47–6.33	5.88 ± 0.18 5.58–6.15	6.38 —	6.10 ± 0.13 5.97–6.38	6.06 ± 0.13 5.80–6.23
Zygomatic breadth	17.96 —	18.21 ± 0.47 (12) 17.36–18.99	18.22 ± 0.38 17.69–18.91	18.03 —	17.19 ± 0.48 16.44–18.03	17.12 ± 0.23 16.81–17.62
Mastoid breadth	14.26 —	14.29 ± 0.41 (12) 13.71–15.09	14.25 ± 0.28 13.71–14.55	14.47 —	14.20 ± 0.15 (8) 14.02–14.47	14.04 ± 0.18 13.77–14.29
Nasal length	14.16 —	13.96 ± 0.47 (12) 13.06–14.64	13.99 ± 0.40 13.40–14.81	14.02 —	14.15 ± 0.28 13.78–14.70	14.02 ± 0.40 13.55–14.71
Incisive foramen length	5.32 —	5.20 ± 0.23 (12) 4.84–5.53	5.14 ± 0.27 4.72–5.51	5.04 —	5.12 ± 0.12 4.92–5.30	5.01 ± 0.18 4.60–5.23
Rostral depth	7.45 —	7.46 ± 0.22 (12) 7.10–7.75	7.47 ± 0.20 7.23–7.87	6.78 —	6.63 ± 0.13 6.40–6.78	6.71 ± 0.14 6.43–6.86
Rostral length	14.96 —	14.96 ± 0.45 (12) 14.17–15.70	15.11 ± 0.36 14.64–15.85	15.72 —	15.37 ± 0.29 15.03–15.72	15.28 ± 0.35 14.73–15.86
Orbitotemporal length	12.03 —	11.99 ± 0.27 (12) 11.56–12.38	11.88 ± 0.41 11.13–12.35	11.29 —	11.07 ± 0.17 10.92–11.37	10.87 ± 0.30 10.39–11.34
Maxillary toothrow length	6.81 —	6.83 ± 0.21 6.47–7.19	6.78 ± 0.19 6.52–7.09	6.64 —	6.63 ± 0.16 6.45–6.94	6.67 ± 0.14 6.48–6.95
Labial palatal breadth at M^1	7.35 —	7.38 ± 0.19 (12) 7.03–7.70	7.43 ± 0.12 7.18–7.60	7.43 —	7.19 ± 0.18 6.90–7.43	7.28 ± 0.17 7.05–7.55
Diastema length	9.00 —	9.33 ± 0.31 (12) 8.95–9.86	9.35 ± 0.36 8.81–9.89	9.80 —	9.57 ± 0.14 9.42–9.82	9.59 ± 0.21 9.38–9.97
Postpalatal length	12.11 —	11.88 ± 0.34 (12) 11.25–12.53	11.80 ± 0.29 11.38–12.18	11.87 —	11.24 ± 0.34 10.88–11.87	11.15 ± 0.24 10.81–11.50
Lingual palatal breadth at M^3	4.87 —	4.96 ± 0.22 (12) 4.51–5.30	5.07 ± 0.22 4.69–5.44	4.90 —	4.86 ± 0.08 4.73–4.93	4.89 ± 0.16 4.68–5.22
Braincase height	11.21 —	10.80 ± 0.39 (12) 10.02–11.44	10.88 ± 0.26 10.55–11.35	10.53 —	10.69 ± 0.21 10.38–10.96	10.53 ± 0.18 10.13–10.82
Breadth of M^1	1.84 —	1.91 ± 0.07 1.77–2.05	1.87 ± 0.06 1.78–1.98	1.82 —	1.80 ± 0.06 1.70–1.87	1.81 ± 0.04 1.74–1.87
Breadth of incisors at tip	2.07 —	2.14 ± 0.12 (12) 1.95–2.34	2.26 ± 0.11 2.09–2.42	1.98 —	1.97 ± 0.05 1.91–2.05	1.99 ± 0.08 1.85–2.10
Width of zygomatic plate	3.31 —	3.25 ± 0.19 (12) 2.94–3.52	3.08 ± 0.13 2.94–3.35	3.57 —	3.35 ± 0.15 3.15–3.57	3.40 ± 0.17 3.09–3.67
Length of head and body	137 —	137.9 ± 7.5 (11) 125–154	137.3 ± 4.9 (10) 128–143	145 —	138.2 ± 4.4 132–145	135.3 ± 5.0 (9) 128–141
Total length	266 —	265.8 ± 10.4 (11) 250–287	261.6 ± 8.0 (10) 250–271	278 —	269.2 ± 6.3 260–279	260.7 ± 9.1 246–275
Length of tail vertebrae	129 —	127.9 ± 4.8 (11) 118–133	124.3 ± 5.9 (10) 111–130	133 —	131.0 ± 3.6 126–138	125.2 ± 5.9 (9) 116–134
Length of hind foot	37 —	36.5 ± 0.8 (11) 35–37	35.7 ± 1.2 (10) 33–37	34 —	33.2 ± 1.1 31–34	33.4 ± 0.8 32–35
Length of ear	23 —	23.2 ± 0.6 (12) 22–24	23.3 ± 0.7 (10) 22–24	18 —	18.2 ± 0.4 18–19	18.2 ± 0.4 18–19
Weight (g)	80 —	78.8 ± 5.9 (12) 71–92	80.1 ± 4.3 (10) 72–86	92 —	76.9 ± 7.8 66–92	73.7 ± 7.0 66–86

(Figs. 3, 14, 15; Balete et al., this volume), and we suspect that it occurs up to the top of the peak at 1910 m. At our two upper sampling areas (1681 and 1785 m), it was the only species of *Megapomys* present. At 1677 m, one of 25 specimens was an *A. aurorae* sp. nov., and at 1540 m one of nine *Megapomys* was *A. aurorae* sp. nov. At 1305, 1074, 902, and 733 m, only *A. aurorae* sp. nov. were captured. We suspect that *A. minganensis* is widespread in the Mingan Mountains above about 1500 m. Our surveys to the north of the Mingan Mountains, in the southern portions of the central Sierra Madre, yielded only specimens of *A. sierrae* sp. nov., and so we consider it unlikely that *A. minganensis* occurs there. No information on small mammals is currently available from the Dingalan Mountains, just to the south of the Mingan Mountains, or from the peaks of the southern Sierra Madre range in Rizal and adjacent Quezon provinces; surveys there would be valuable to determine whether this species is present, or whether yet more unknown species are present. If this species is indeed confined to the high elevations of the Mingan Mountains, it has one of the smaller ranges among species of *Apomys*.

Apomys (*Megapomys*) *sierrae* sp. nov.

HOLOTYPE—FMNH 185884, adult male collected on 15 June 2005 by Mariano Roy M. Duya, field number MRMD 354B. A sample of muscle tissue was removed from the thigh in the field and preserved in ethanol before preserving the specimen

TABLE 9. *Extended.*

Apomys sierrae				
Mt. Cetaceo, 1300–1400 m, Cagayan Prov.			**Mt. Cetaceo, 1500–1550 m, Cagayan Prov.**	
M-holotype FMNH 185884	**M (n = 8)**	**F (n = 4)**	**M (n = 12)**	**F (n = 10)**
35.40	35.15 ± 0.46	35.24 ± 0.46	35.31 ± 0.57	35.30 ± 0.50
—	34.32–35.86	34.69–35.64	34.68–36.43	34.70–36.25
6.22	6.09 ± 0.13	6.06 ± 0.33	6.44 ± 0.22	6.30 ± 0.17
—	5.90–6.25	5.58–6.29	6.15–6.77	5.95–6.46
17.89	18.10 ± 0.48	18.24 ± 0.78	18.29 ± 0.48	18.21 ± 0.39
—	17.32–18.99	17.39–18.95	17.60–19.39	17.58–18.76
14.22	14.20 ± 0.27	14.29 ± 0.19	14.61 ± 0.28	14.38 ± 0.34
—	13.78–14.75	14.03–14.45	14.21–15.21	13.68–14.76
14.29	14.05 ± 0.35	13.88 ± 0.39	14.21 ± 0.59 (11)	14.15 ± 0.21
—	13.45–14.61	13.36–14.25	13.49–15.55	13.80–14.50
5.60	5.29 ± 0.45	5.33 ± 0.52	5.28 ± 0.22	5.57 ± 0.16
—	4.55–5.79	4.86–5.99	5.00–5.71	5.28–5.77
7.75	7.49 ± 0.16	7.48 ± 0.21	7.63 ± 0.21 (11)	7.51 ± 0.19
—	7.26–7.75	7.19–7.69	7.23–7.84	7.28–7.78
15.52	14.95 ± 0.48	14.86 ± 0.35	15.12 ± 0.55	15.05 ± 0.43
—	14.21–15.52	14.40–15.19	14.40–16.25	14.59–15.75
11.91	12.05 ± 0.20	11.89 ± 0.16	12.02 ± 0.24	12.13 ± 0.34
—	11.84–12.38	11.66–12.03	11.46–12.30	11.73–12.60
7.30	7.66 ± 0.26	7.55 ± 0.17	7.39 ± 0.19	7.47 ± 0.23
—	7.24–7.93	7.38–7.70	7.11–7.70	7.24–7.91
7.68	7.85 ± 0.29	7.87 ± 0.17	7.82 ± 0.39	7.77 ± 0.27
—	7.62–8.45	7.77–8.12	7.19–8.44	7.25–8.05
9.60	9.16 ± 0.36	9.10 ± 0.31	9.52 ± 0.30	9.56 ± 0.29
—	8.61–9.60	8.81–9.48	9.02–10.00	9.03–10.04
11.92	11.63 ± 0.29	11.60 ± 0.18	11.77 ± 0.28	11.76 ± 0.31
—	11.07–11.92	11.46–11.86	11.21–12.10	11.24–12.26
5.62	5.47 ± 0.21	5.46 ± 0.10	5.44 ± 0.26	5.42 ± 0.22
—	5.17–5.81	5.35–5.55	4.87–5.66	5.10–5.84
10.66	10.63 ± 0.16 (7)	10.72 ± 0.17	10.90 ± 0.31	10.80 ± 0.41
—	10.38–10.78	10.51–10.91	10.41–11.40	9.85–11.30
1.90	1.93 ± 0.09	1.89 ± 0.09	1.91 ± 0.07	1.89 ± 0.08
—	1.82–2.04	1.80–1.97	1.83–2.02	1.73–2.03
2.28	2.16 ± 0.10 (7)	2.11 ± 0.08	2.28 ± 0.09	2.30 ± 0.12
—	1.98–2.28	2.04–2.22	2.14–2.40	2.06–2.53
3.68	3.58 ± 0.26	3.67 ± 0.12	3.56 ± 0.21	3.48 ± 0.25
—	3.34–4.19	3.50–3.77	3.29–3.85	3.07–3.87
131	133.4 ± 6.4	140.8 ± 6.8	143.3 ± 8.7 (10)	140.6 ± 4.2 (9)
—	124–144	134–148	132–163	135–146
271	267.1 ± 6.2	276.3 ± 4.6	274.4 ± 12.5 (10)	272.1 ± 7.9 (9)
—	254–273	271–282	260–295	260–281
140	133.8 ± 4.4	135.5 ± 5.0	131.6 ± 6.7 (11)	131.6 ± 6.4 (9)
—	129–140	129–141	124–148	118–137
37	35.5 ± 1.0	35.1 ± 0.9	36.7 ± 1.2	35.7 ± 1.0 (9)
—	34–37	34–36	35–39	34–37
19	19.0 ± 0.9	19.6 ± 1.0	20.2 ± 0.6	19.7 ± 0.7 (9)
—	18–21	18–20	19–21	18–20
90	84.5 ± 5.9	81.5 ± 6.6	84.9 ± 9.5 (11)	77.2 ± 4.6 (9)
—	73–92	74–88	75–110	72–85

in formaldehyde. In the museum, the skull was removed and cleaned (see Methods). All parts are in good condition. This specimen will be permanently deposited at the NMP. Measurements appear in Table 9.

TYPE LOCALITY—Philippines: Luzon: Cagayan Province: 3.5 km SW Mt. Cetaceo peak, 1400 m elevation, 17.69561°N, 122.01683°E.

PARATYPES (n = 408)—Luzon Island: Cagayan Prov.: 1.5 km SW Mt. Cetaceo peak, 1550 m (FMNH 185834–185841, 185861–185880, 185900, 185946, 185961); 2.0 km SW Mt. Cetaceo peak, 1500 m (FMNH 185805, 185815–185833, 185842–185845, 185854–185860, 185896–185898, 185904, 185905, 185938–185945, 185955–185960); 3.5 km SW Mt. Cetaceo peak, 1400 m (FMNH 185803–185814, 185846–185853, 185881, 185883, 185885–185895, 185899, 185901–185903, 185906, 185936, 185937, 185947–185954, 185962–185970); Baggao Munic.: Barrio Via, Sitio Hot Springs, W Foothills Sierra Madre Mtns., 760–800 m (USNM 574889); Callao Munic.: Mt. Cetaceo, 1450 m (FMNH 147166–147169); Gonzaga Munic.: Brgy. Magrafil: Sitio Masok: Mt. Cagua, 800 m (FMNH 176562–176576); Penablanca Munic.: Brgy. Lapi: Sitio Baua: Mt. Cetaceo, 1300 m (FMNH 180298–180364); Penablanca Munic.: Brgy. Mangga: Sitio Lowak: Mt. Cetaceo, 1100 m (FMNH 176552–176558).

Isabela Prov.: Los Dos Cuernos, E of Tuguegarao (FMNH 142060); Mt. Dipalayag, E of San Mariano (FMNH 142061, 142062).

Nueva Vizcaya Prov.: Quezon Munic.: 0.8 km N, 0.55 km E Mt. Palali peak, 1420 m (FMNH 186726–186760, 186778, 186786, 186820–186825,194934–194947); Quezon Munic.:

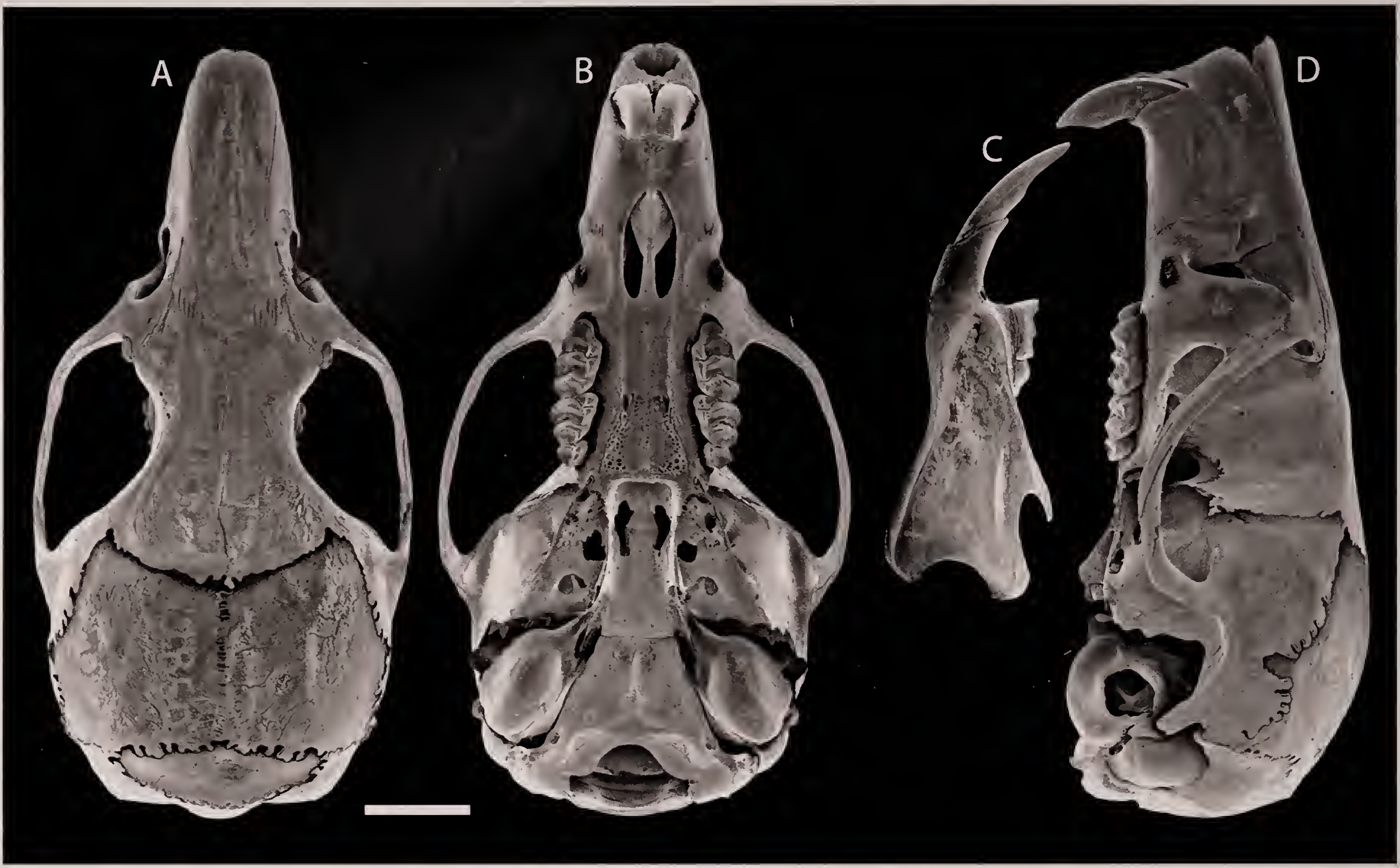


Fig. 28. Dorsal (**A**), ventral (**B**), and lateral (**D**) views of the cranium and lateral view of the mandible (**C**) of *Apomys banahao* sp. nov. (FMNH 178501, holotype); scale bar = 5 mm.

1.75 km N, 0.1 km E Mt. Palali peak, 1300 m (FMNH 194948–194961); Quezon Munic.: 2.75 km N, 0.3 km W Mt. Palali peak, 1040 m (FMNH 194962–194977); Quezon Munic.: 3.05 km N, 0.1 km E Mt. Palali peak, 900 m (FMNH 194978–194998); Quezon Munic.: 3.35 km N, 0.5 km W Mt. Palali peak, 780 m (FMNH 194999–195015); Quezon Munic.: Mt. Palali peak, 1700 m (FMNH 186761–186777, 186779–186785, 186826, 186827, 194923–194933).

Quirino Prov.: Nagtipunan Munic.: Brgy. Disimungal: Sitio Km 18: Mt. Lataan, 1200 m (FMNH 176559–176561); Nagtipunan Munic.: Brgy. Matmad: Sitio Mangitagud: Mungiao Mtns., 450 m (FMNH 180365–180373).

Palaui Island: Cagayan Prov.: Sta. Ana Munic.: Brgy. San Vicente: 4.25 km S of Cape Engano Lighthouse, 153 m (FMNH 191232–191237).

Etymology—From the name of the mountain range (Sierra Madre) where most of the specimens of this species originated, used as a noun in the genitive case.

Diagnosis and Description—A species of the subgenus *Megapomys* of average size (HBL 124–171 mm, averaging

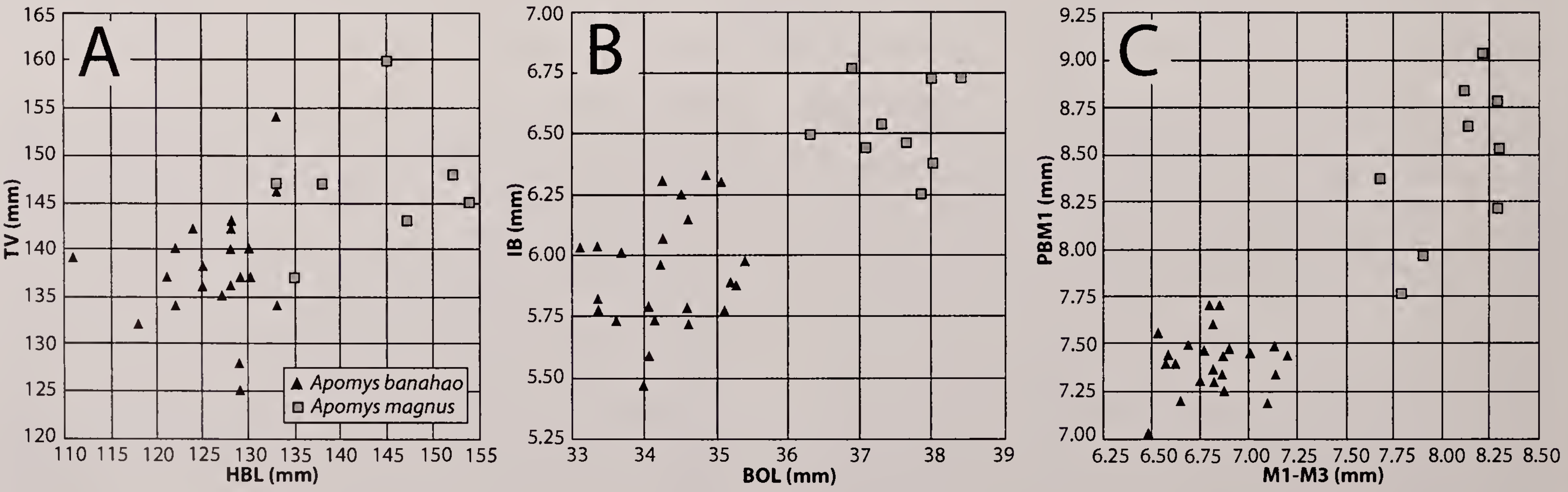


Fig. 29. Bivariate plots of measurements comparing *Apomys banahao* and *A. magnus* spp. nov. (**A**) Head and body length (HBL) and length of tail vertebrae (TV). (**B**) Basioccipital length (BOL) and interorbital breadth (IB). (**C**) Length of maxillary molariform toothrow (M^1–M^3) and labial palatal breadth at M^1 (PBM^1).

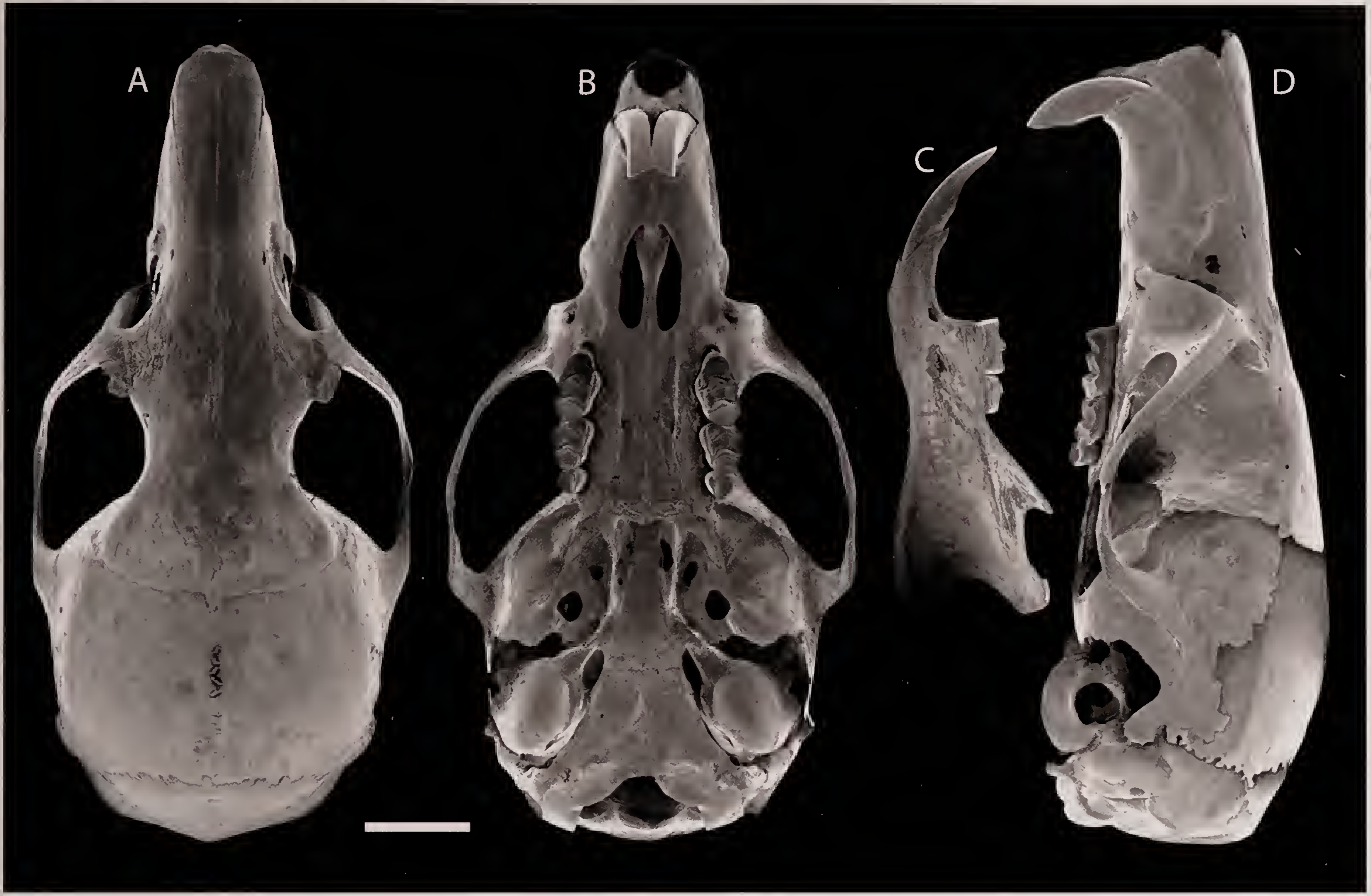


FIG. 30. Dorsal (**A**), ventral (**B**), and lateral (**D**) views of the cranium and lateral view of the mandible (**C**) of *Apomys minganensis* sp. nov. (FMNH 190949, holotype); scale bar = 5 mm.

133–150 mm; weight 73–111 g, averaging 79–88 g), with a tail that is about equal to the HBL (85–111%, averaging 95–102%). In the Sierra Madre range, the dorsal pelage is dark brown with conspicuous rusty-reddish tints (Fig. 2C); on Mt. Palali in the Caraballo Mountains, the dorsal pelage is a medium brown with yellow tint, and the skin of the ears and feet are paler than in individuals from the Sierra Madre (Fig. 2D). The ventral pelage is medium to pale gray at the base and white or white washed with pale ochraceous at the tips. The tail is sharply bicolored, dark brown dorsally (somewhat paler on individuals from Mt. Palali) and usually white (unpigmented) ventrally. As with most species of *Apomys*, a few individuals (less than 5%) have a white tip on the tail. The dorsal surface of the hind foot of *A. sierrae* is mostly white, with only a few scattered dark hairs. The ventral surface is moderately to darkly pigmented (darker on those

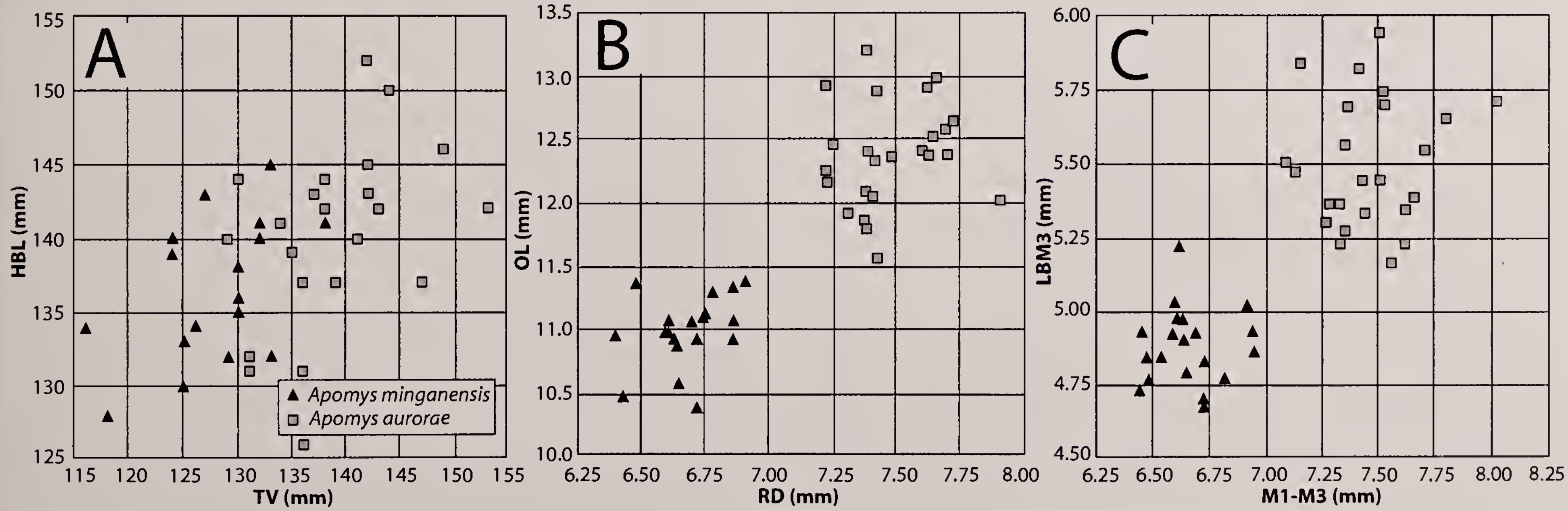


FIG. 31. Bivariate plots of measurements comparing *Apomys minganensis* and *A. aurorae* spp. nov. (**A**) Length of tail vertebrae (TV) and length of head and body (HBL). (**B**) Rostral depth (RD) and orbitotemporal length (OL). (**C**) Length of maxillary molariform toothrow (M^1–M^3) and lingual breadth of palate at M^3 (LBM^3).

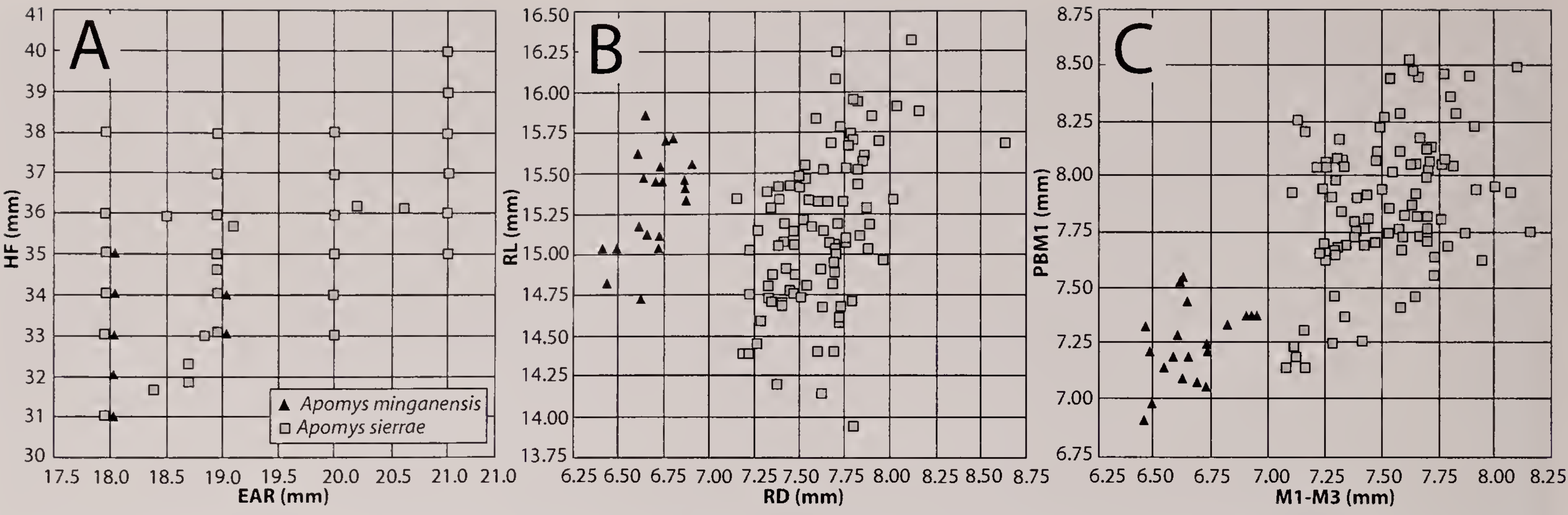


FIG. 32. Bivariate plots of measurements comparing *Apomys minganensis* and *A. sierrae* spp. nov. (**A**) Length of ear (EAR) and length of hind foot (HF). (**B**) Rostral depth (RD) and rostral length (RL). (**C**) Length of the maxillary toothrow (M^1–M^3) and labial palatal breadth at M^1 (PBM^1).

from the Sierra Madre than from Mt. Palali), with relatively small plantar pads, and the hallux is short, usually extending only to about the base of the adjacent interdigital plantar pad (Fig. 10E).

The skull of *A. sierrae* (Fig. 34) is of average size within *Megapomys* (BOL 33.5–37.5 mm, with individual populations averaging 35.1–36.1 mm; Tables 9, 11, 12). It is most similar overall to several of the species to which it is most closely related: *A. aurorae* sp. nov., *A. minganensis*, and *A. zambalensis* sp. nov. (*Apomys magnus* sp. nov. is much larger and differs in other respects.) The rostrum is rather long and slender, and the braincase is globose and slightly elongated. The maxillary molar teeth are rather narrow, and the toothrows diverge posteriorly. The palate is unusually heavily perforated and pitted, and the postpalatal region is of average length. The foramen for the stapedial artery in the bulla is absent (the "abrae pattern"; Fig. 5A). The interparietal is usually anteroposteriorly wide. The mandible (Fig. 34C) is rather slender. The coronoid process is relatively erect (less posteriorly directed) and sharply pointed, the angular process is relatively narrow, and the posterior margin between the condylar and angular processes is deeply concave.

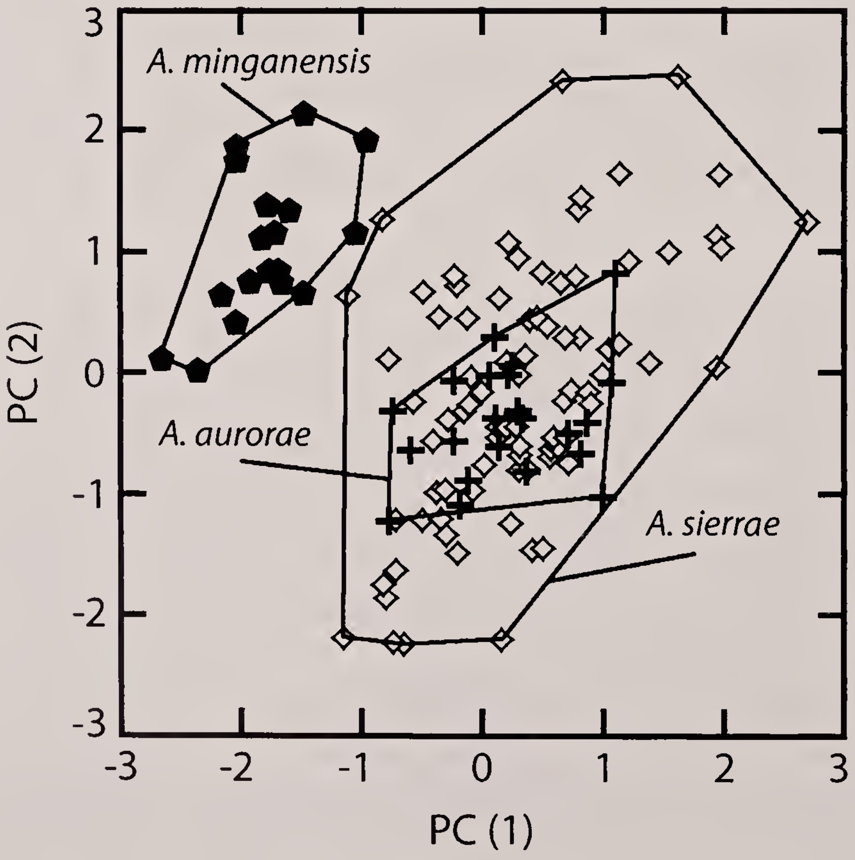


FIG. 33. Results of the principal components analysis of *Apomys aurorae*, *A. minganensis*, and *A. sierrae* spp. nov. (see text and Table 10) based on specimens in Tables 9, 11, 12, and 15.

As noted above, our samples from Cagayan, Quirino, and Nueva Vizcaya provinces show no geographic pattern of genetic relatedness, even though they come from distant mountains and from Palaui Island (Figs. 3, 7, 35). Our sample from Palaui Island showed slight genetic differentiation (Fig. 7), and cranial measurements are slightly smaller than those on the nearby mainland (Tables 9, 11, 12), but the latter is explained in part by the fact that all three Palaui Island specimens were young animals with partially open cranial sutures and had not completed growth. Specimens from Nueva Vizcaya have paler fur than those from Cagayan and Quirino but are otherwise externally indistinguishable. Comparison of measurements (Tables 9, 11, 12) shows extensive overlap of individuals from all of our samples, and we have noted no discrete cranial differences among them.

To further investigate possible divergence within the set of populations here referred to *A. sierrae*, we conducted a PCA of 18 craniodental measurements of the individuals included in Tables 9, 11, and 12. In this analysis, we broke our samples not only into those from each geographic locality, but also designated them by groups on the basis of elevation along the Mt. Cetaceo and Mt. Palali transects because often two species of *Megapomys* are present at different elevations on Luzon mountains (see Discussion). The first PC, which accounted for 34% of the total variance, loaded heavily on all measurements except length of upper molar toothrow, breadth of M^1, and height of braincase (Table 13), thus generally indicating size and robustness. The second component, which accounted for 14% of the variance, loaded heavily on length of upper molar toothrow, palatal breadth at M^1, and breadth of M^1; diastema length and postpalatal length loaded negatively. Subsequent components had eigenvalues of less than 1.5.

Inspection of the scores of individuals on the first two components (Fig. 36) shows nearly complete overlap on the first component, with six individuals from Mt. Palali scoring outside of the primary range of values (i.e., scoring higher than 1.5 on PC1). These individuals (FMNH 186777, 194926, 194970,

Table 10. Character loadings, eigenvalues, and percent variance explained on the first four components of a principal components analysis of log-transformed measurements of adult *Apomys aurorae, A. minganensis,* and *A. sierrae* (see Fig. 33 and Methods).

Variable	Principal component			
	1	2	3	4
Basioccipital length	0.828	0.332	−0.092	0.261
Interorbital breadth	0.427	0.490	−0.325	−0.276
Zygomatic breadth	0.836	−0.005	0.050	−0.130
Mastoid breadth	0.619	0.245	0.041	−0.333
Nasal length	0.487	0.459	0.343	−0.242
Incisive foramen length	0.566	0.019	0.192	0.228
Rostral depth	0.854	−0.165	0.049	0.072
Rostral length	0.330	0.698	0.334	−0.180
Orbitotemporal length	0.823	−0.156	−0.131	0.239
Maxillary toothrow length	0.692	−0.576	−0.071	0.036
Labial palatal breadth at M^1	0.829	−0.276	0.266	−0.203
Diastema length	0.245	0.758	0.073	0.224
Postpalatal length	0.592	0.386	−0.303	0.344
Lingual palatal breadth at M^3	0.753	−0.222	0.153	0.008
Braincase height	0.321	0.035	−0.666	−0.477
Breadth of M^1	0.520	−0.529	0.229	−0.291
Breadth of incisors at tip	0.676	−0.160	−0.320	0.110
Width of zygomatic plate	0.439	−0.172	0.031	0.262
Eigenvalue	7.191	2.679	1.200	1.081
Percent variance explained	39.95	14.88	6.67	6.01

195007, 195014, 195015) have unusually heavily worn teeth and skulls that are more robust than usual; they appear simply to be "old adults" that are otherwise not distinguishable from other individuals from Mt. Palali. On PC2, individuals from Palaui Island, two from Mt. Cagua (which is the sample on mainland Luzon nearest to Palaui Island; Figs. 3, 35) and four from Mt. Cetaceo, score near one another, outside of the primary range of values (i.e., they have scores lower than −1.5). As noted above, the three from Palaui Island are young adults that have not fully completed growth; the same is true for the two from Cagua and four from Cetaceo that have low scores. The differences in measurements are largely those associated with unworn teeth. We note no differences in the crania that are not associated with their young age.

Aside from variation associated with these outliers, which we ascribe to age-related differences, all individuals assigned here to *A. sierrae* fall in a tight area of overlap in the plot of PC1 vs. PC2, and we conclude that craniodental morphometric variation is slight. Because the extent of geographic variation in cyt *b* also is slight, we hypothesize that all of these populations represent a single, widespread species.

Comparisons—*Apomys sierrae* is easily distinguished from its close relative *A. minganensis*, as described in detail above (Fig. 32); *A. minganensis* has longer, denser, and darker dorsal fur and many dark hairs on the dorsal surface of the hind foot, and the hallux is long, reaching nearly to the top of the adjacent plantar pad, rather than reaching only to the bottom of the pad as in *A. sierrae*. The skull has a shorter toothrow with narrower molars and a foramen in the bulla for the stapedial artery that is relatively large and conspicuous, rather than absent (Fig. 5). A PCA of craniodental measurements comparing *A. sierrae* with *A. minganensis* also showed discrete differences (Fig. 33; Table 10; see *A. minganensis* account, above).

Apomys sierrae differs from *A. magnus* sp. nov., to which it is closely related, by usually being smaller (e.g., HBL averaging 133–150 mm vs. 145–148 mm, BOL 35.1–36.1 mm vs. 37.0–37.7 mm). The dorsal pelage of *A. sierrae* (Fig. 2C,D) is dark brown with rusty reddish tones or a rich rusty orange-brown, whereas that of *A. magnus* (Fig. 1E) is dark brown with prominent black guard hairs and virtually no reddish tones. Ventrally, *A. sierrae* has fur that is dark gray at the base and pale gray at the tip with an ochraceous wash, whereas that of *A. magnus* sp. nov. is somewhat paler gray at the base and nearly white at the tip. The ventral surface of the hind foot is usually darkly pigmented in both species, but the hallux of *A. magnus* sp. nov. is longer, reaching nearly to the top of the adjacent plantar pad, rather than only to its base (Fig. 10D,E). A comparison of hind foot length against weight for the two species shows little overlap (Fig. 37A).

The crania of *A. sierrae* and *A. magnus* sp. nov. differ conspicuously. That of *A. magnus* is generally larger and more robust, with little overlap in basioccipital length, interorbital breadth, zygomatic breadth, mastoid breadth, nasal length, length of the incisive foramina, length of the maxillary toothrows, and palatal breadth. Plots of orbital length against postpalatal length, and of rostral length against depth, show good but not complete separation among nearly all individuals (Fig. 37B,C); additionally, the stapedial foramen in the bulla is large and conspicuous in *A. magnus* (the "datae pattern"; Fig. 5B) but absent in *A. sierrae* (the "abrae pattern"; Fig. 5A), allowing easy identification of skulls.

To further investigate differences between *A. sierrae* and *A. magnus* sp. nov. and the closely related *A. zambalensis* sp. nov., we conducted a PCA of 18 craniodental measurements. The first principal component (PC1), which accounted for 40% of the total variance, loaded heavily on nearly all measurements, indicating that this is largely an indicator of size and robustness; only width of zygomatic plate and breadth of M^1 loaded less strongly (Table 14). PC2 loaded strongly (and positively) on length of the upper molar toothrow, palatal breadth at M^1, and breadth of M^1 and strongly (but negatively) on diastema length and postpalatal length. Subsequent components had eigenvalues less than 1.2. A plot of PC1 and PC2 (Fig. 38) shows that *A. magnus* sp. nov. scored higher than *A. sierrae* on PC1 with limited overlap, confirming its generally large size. There was complete overlap on PC2. As noted below, *A sierrae* is easily distinguished from *A. zambalensis* sp. nov. with the use of qualitative features and some craniodental features; this morphometric analysis shows that they do not differ in overall size, but they generally differ on PC2, although with overlap, confirming the utility of dental measurements, diastema length, and postpalatal length in distinguishing most individuals, as discussed below. Given the extent of morphological and genetic differences among these species, we regard each as distinct from the others.

Apomys sierrae differs from *A. aurorae* sp. nov., its closest geographic neighbor, usually in subtle ways, reflecting the relatively close phylogenetic relationship evident in Figure 7. Their external dimensions are similar; *A. sierrae* tends to have a longer hind foot, but the means of other measurements are similar (Fig. 39A; Tables 9, 11, 12, 15). The dorsal pelage is rusty brown on both species, but has more of a yellow tint in *A. aurorae* sp. nov. (Fig. 2F) and a more reddish tint in *A. sierrae* (Fig. 2C). The ventral pelage of the two species is similar. Dark hairs extend down further on the forelimbs of *A. sierrae*, reaching the base of the paws, whereas there is only white fur on the lower forelimbs and forepaws of *A. aurorae* sp. nov. The dorsal surface of the hind foot of *A. sierrae* is

Table 11. Cranial and external measurements (mean ± 1 S.D. and range) of *Apomys sierrae* (part).

	Apomys sierrae					
	Mt. Cagua, 800 m, Cagayan Prov.		**Mt. Lataan, 1200 m, Quirino Prov.**		**Mungiao Mtns., 450 m, Quirino Prov.**	
Measurement	**M (n = 4)**	**F (n = 1)**	**M (n = 1)**	**F (n = 2)**	**M (n = 2)**	**F (n = 3)**
Basioccipital length	35.70 ± 1.44 (3)	35.98	—	35.18 ± 1.09	34.60 (1)	34.73 ± 0.75 (2)
	34.67–37.35	—	—	34.41–35.95	—	34.20–35.26
Interorbital breadth	6.17 ± 0.26	6.30	—	5.98 ± 0.11	6.15 ± 0.25	6.15 ± 0.04 (2)
	5.82–6.41	—	—	5.90–6.05	5.97–6.32	6.12–6.18
Zygomatic breadth	17.52 ± 0.42	17.66	—	17.93 ± 0.89	18.24 ± 0.47	18.06 ± 0.23 (2)
	16.97–17.96	—	—	17.30–18.56	17.90–18.57	17.89–18.22
Mastoid breadth	14.14 ± 0.18	14.23	—	13.68 ± 0.35	14.27 ± 0.13	14.06 ± 0.69 (2)
	14.02–14.41	—	—	13.43–13.93	14.18–14.36	13.57–14.54
Nasal length	14.67 ± 0.50 (3)	15.12	—	14.49 ± 0.17	14.36 (1)	14.27 ± 0.02 (2)
	14.36–15.24	—	—	14.37–14.61	—	14.25–14.28
Incisive foramen length	5.30 ± 0.08 (3)	5.87	—	4.96 ± 0.06	5.24 (1)	5.73 ± 0.01 (2)
	5.23–5.39	—	—	4.91–5.00	—	5.72–5.73
Rostral depth	7.57 ± 0.19 (3)	7.70	—	7.55 ± 0.47	7.40 (1)	7.79 ± 0.11 (2)
	7.42–7.78	—	—	7.22–7.88	—	7.71–7.86
Rostral length	15.45 ± 0.27 (3)	15.19	—	15.03 ± 0.01	14.70 (1)	14.95 ± 0.49 (2)
	15.19–15.72	—	—	15.02–15.03	—	14.60–15.29
Orbitotemporal length	12.16 ± 0.32	12.84	—	12.21 ± 0.32	12.13 ± 0.71	12.14 ± 0.09 (2)
	11.76–12.48	—	—	11.98–12.43	11.63–12.63	12.08–12.20
Maxillary toothrow length	7.41 ± 0.22	7.29	7.69	7.64 ± 0.01	7.72 ± 0.27	8.01 ± 0.17
	7.15–7.60	—	—	7.63–7.65	7.53–7.91	7.82–8.15
Labial palatal breadth at M^1	7.57 ± 0.23	7.98	7.81	7.76 ± 0.42	8.05 ± 0.26	7.98 ± 0.26
	7.31–7.83	—	—	7.46–8.05	7.86–8.23	7.75–8.27
Diastema length	9.62 ± 0.69 (3)	9.99	—	9.52 ± 0.50	9.06 (1)	9.13 ± 0.21 (2)
	8.83–10.12	—	—	9.17–9.87	—	8.98–9.27
Postpalatal length	11.88 ± 0.62	11.82	—	11.70 ± 0.51	11.81 ± 0.29	11.19 ± 0.25 (2)
	11.50–12.81	—	—	11.34–12.06	11.60–12.01	11.01–11.36
Lingual palatal breadth at M^3	5.24 ± 0.04	5.33	—	5.42 ± 0.34	5.37 ± 0.33	5.49 ± 0.33 (2)
	5.20–5.30	—	—	5.18–5.66	5.13–5.60	5.26–5.72
Braincase height	10.99 ± 0.33	10.45	—	10.54 ± 0.62	10.81 ± 0.72	10.64 ± 0.16 (2)
	10.63–11.35	—	—	10.10–10.97	10.30–11.32	10.52–10.75
Breadth of M^1	1.81 ± 0.11	1.94	1.97	1.99 ± 0.00	2.04 ± 0.04	2.03 ± 0.07
	1.70–1.93	—	—	1.99	2.01–2.07	1.95–2.08
Breadth of incisors at tip	2.19 ± 0.07 (3)	2.30	—	2.34 ± 0.02	2.19 (1)	2.24 ± 0.06 (2)
	2.12–2.26	—	—	2.32–2.35	—	2.19–2.28
Width of zygomatic plate	3.50 ± 0.20	3.59	—	3.79 ± 0.01	3.85 ± 0.00	3.61 ± 0.22 (2)
	3.22–3.69	—	—	3.78–3.80	3.85	3.45–3.76
Length of head and body	132.4 ± 9.4 (3)	—	133	149 (1)	143.0 ± 8.5	134.7 ± 4.0
	122–141	—	—	—	137–149	131–139
Total length	271.0 ± 19.3 (3)	277	262	296 (1)	286.5 ± 19.1	274.0 ± 12.3
	250–288	—	—	—	273–300	265–288
Length of tail vertebrae	138.6 ± 9.9 (3)	—	129	139.3 ± 10.3	143.5 ± 10.6	139.3 ± 8.4
	128–147	—	—	132–147	136–151	134–149
Length of hind foot	33.2 ± 1.8	32	33	34.0 ± 0.0	36.5 ± 2.1	35.0 ± 2.0
	32–36	—	—	34	35–38	33–37
Length of ear	18.8 ± 0.3	19	20	20.0 ± 0.0	21.0 ± 0.0	20.0 ± 1.0
	18–19	—	—	20	21	19–21
Weight (g)	84.3 ± 8.3	106	66	79.0 ± 17.0	86.0 ± 14.1	79.3 ± 13.6
	78–96	—	—	67–91	76–96	64–90

primarily white, with a few scattered dark hairs, whereas that of *A. aurorae* sp. nov. is either white or has scattered dark hairs, except for having pure white adjacent to and on the toes. Both species have a short hallux that reaches only about to the bottom of the adjacent plantar pad. The two species are most readily distinguished on the basis of the basicranial carotid circulatory pattern. In *A. sierrae*, the foramen for the stapedial artery in the bulla is absent (the "abrae pattern"; Fig. 5A), whereas in *A. aurorae* sp. nov., it is small but always present (the "datae pattern"; Fig. 5B). The configuration of the skulls is similar, and the PCA of cranial measurements shows that individuals of *A. aurorae* sp. nov. fall entirely within the plots of *A. sierrae* (Fig. 33; Table 10). However, close inspection shows the skull of *A. sierrae* is slightly more elongate, usually with a slightly shorter rostrum and orbitotemporal fossa (Fig. 39C), and a braincase that is less broad. The maxillary toothrows of *A. sierrae* usually are slightly narrower and they diverge posteriorly to a greater degree than in *A. aurorae* sp. nov. The zygomatic plate of *A. sierrae* tends to be narrower than that of *A. aurorae* sp. nov. (Figs. 34, 39B). The interparietal bones of the two species are variable, but usually similar in width. The mandible of *A. aurorae* sp. nov. is slightly deeper, and the posterior margin between the condylar and angular processes is less concave. Although most differences are slight, the discrete difference in the form of the carotid circulatory system and the genetic monophyly of the two

TABLE 11. *Extended.*

Apomys sierrae					
Mt. Palali, 700–839 m, Nueva Vizcaya Prov.		Mt. Palali, 1052–1259 m, Nueva Vizcaya Prov.		Mt. Palali, 1434–1443 m, Nueva Vizcaya Prov.	
M (n = 7)	F (n = 2)	M (n = 2)	F (n = 4)	M (n = 8)	F (n = 12)
36.13 ± 0.78 (6)	35.25 ± 0.40	35.19 ± 2.01	34.57 ± 0.70	34.68 ± 0.75	35.07 ± 0.70
35.52–37.52	34.97–35.53	33.77–36.61	33.55–35.12	33.49–35.63	34.44–36.80
6.23 ± 0.19 (6)	6.24 ± 0.21	6.13 ± 0.46	6.13 ± 0.38	6.05 ± 0.19	5.91 ± 0.16
6.05–6.54	6.09–6.38	5.80–6.45	5.57–6.38	5.76–6.32	5.64–6.22
18.76 ± 0.50 (6)	17.75 ± 0.26	18.47 ± 0.71	18.34 ± 0.80	18.18 ± 0.22	18.36 ± 0.55
18.05–19.55	17.56–17.93	17.96–18.97	17.45–19.18	17.84–18.58	17.42–19.48
14.83 ± 0.59 (6)	14.21 ± 0.27	14.78 ± 0.21	14.30 ± 0.48	14.43 ± 0.16	14.45 ± 0.38
13.99–15.36	14.02–14.40	14.63–14.92	13.97–15.01	14.28–14.73	13.88–15.35
15.15 ± 0.29 (6)	15.03 ± 0.40	14.44 ± 0.73	14.03 ± 0.53	14.26 ± 0.41	14.43 ± 0.37
14.70–15.46	14.75–15.31	13.92–14.95	13.58–14.73	13.49–14.83	13.76–15.03
5.98 ± 0.27 (6)	5.35 ± 0.08	5.47 ± 0.06	5.35 ± 0.26	5.41 ± 0.34	5.40 ± 0.31
5.57–6.34	5.29–5.40	5.43–5.51	5.02–5.57	4.68–5.78	4.78–5.84
8.03 ± 0.35 (6)	7.74 ± 0.27	7.75 ± 0.40	7.50 ± 0.20	7.57 ± 0.19	7.55 ± 0.16
7.68–8.63	7.55–7.93	7.46–8.03	7.21–7.68	7.26–7.80	7.32–7.81
15.98 ± 0.21 (6)	15.53 ± 0.26	15.34 ± 0.82	15.07 ± 0.61	14.87 ± 0.53	15.06 ± 0.39
15.70–16.32	15.35–15.71	14.76–15.92	14.40–15.84	13.95–15.34	14.40–15.69
12.43 ± 0.31 (6)	12.11 ± 0.40	11.95 ± 0.74	12.05 ± 0.32	11.84 ± 0.43	12.07 ± 0.33
12.13–13.03	11.82–12.39	11.43–12.47	11.58–12.30	11.10–12.17	11.39–12.65
7.52 ± 0.31	7.29 ± 0.02	7.51 ± 0.16	7.36 ± 0.18	7.62 ± 0.17	7.61 ± 0.22
7.21–8.09	7.27–7.30	7.39–7.62	7.16–7.60	7.25–7.81	7.13–8.00
8.16 ± 0.29 (6)	7.99 ± 0.11	8.21 ± 0.44	7.97 ± 0.26	7.88 ± 0.18 (7)	7.88 ± 0.20
7.73–8.49	7.91–8.07	7.90–8.52	7.73–8.21	7.62–8.05	7.55–8.25
9.78 ± 0.43 (6)	9.47 ± 0.30	9.09 ± 1.02	9.41 ± 0.50	9.23 ± 0.41	9.33 ± 0.34
9.39–10.51	9.25–9.68	8.37–9.81	8.89–10.09	8.55–9.99	8.97–10.17
11.94 ± 0.59 (6)	11.67 ± 0.21	11.66 ± 0.79	11.29 ± 0.36	11.27 ± 0.47	11.56 ± 0.36
11.35–13.08	11.52–11.82	11.10–12.22	10.80–11.67	10.43–11.89	11.00–12.34
5.55 ± 0.25 (6)	5.57 ± 0.07	5.67 ± 0.46	5.61 ± 0.45	5.51 ± 0.19 (7)	5.39 ± 0.17
5.06–5.77	5.52–5.62	5.34–5.99	5.08–6.15	5.32–5.84	5.10–5.68
10.64 ± 0.39 (6)	10.89 ± 0.06	11.12 ± 0.37	10.50 ± 0.43	10.72 ± 0.22	10.77 ± 0.22
10.07–10.99	10.85–10.93	10.86–11.38	10.01–11.02	10.52–11.10	10.31–11.11
1.96 ± 0.09	1.95 ± 0.12	1.93 ± 0.09	1.93 ± 0.05	1.97 ± 0.04	1.99 ± 0.09
1.87–2.14	1.86–2.03	1.87–1.99	1.87–1.98	1.91–2.04	1.84–2.10
2.17 ± 0.13 (6)	2.12 ± 0.03	2.10 ± 0.32	2.09 ± 0.11	2.13 ± 0.06 (7)	2.30 ± 0.09 (11)
2.05–2.40	2.10–2.14	1.87–2.32	2.02–2.25	2.06–2.22	2.12–2.51
3.65 ± 0.13 (6)	3.35 ± 0.02	3.52 ± 0.45	3.46 ± 0.15	3.50 ± 0.19	3.45 ± 0.27
3.49–3.79	3.33–3.36	3.20–3.83	3.32–3.65	3.18–3.69	2.85–4.05
150.0 ± 11.5 (6)	142.5 ± 0.7	141.5 ± 7.8	138.0 ± 2.2	138.3 ± 6.3	139.1 ± 6.0 (11)
136–171	142–143	136–147	136–141	128–147	130–149
291.7 ± 11.5 (6)	275.0 ± 0.0	278.5 ± 21.9	278.3 ± 7.4	271.0 ± 10.4	276.9 ± 9.9 (11)
275–304	275	263–294	270–287	254–283	254–285
141.7 ± 12.1 (6)	132.5 ± 0.7	137.0 ± 14.1	140.3 ± 5.3	132.8 ± 7.3	137.8 ± 7.0 (11)
124–154	132–133	127–147	134–146	123–146	124–147
36.0 ± 1.8 (6)	36.5 ± 2.1	36.0 ± 0.0	35.8 ± 1.0	35.4 ± 2.1	35.8 ± 1.5
34–39	35–38	36	35–37	31–38	33–38
20.2 ± 1.0 (6)	19.0 ± 1.4	19.0 ± 0.0	19.7 ± 1.2 (3)	19.4 ± 0.9	19.3 ± 0.8
19–21	18–20	19	19–21	18–21	18–20
91.6 ± 12.3 (5)	86.5 ± 10.6	85.0 ± 12.7	74.5 ± 6.4	79.6 ± 7.6	86.8 ± 8.2
80–111	79–94	76–94	70–84	64–90	72–100

groups leads us to hypothesize that they are discrete species, and we treat them as such.

Apomys sierrae is easily distinguished from *A. zambalensis* sp. nov., to which it is also closely related (Fig. 7). *Apomys sierrae* averages smaller in nearly all respects; a plot of ear length and hind foot length shows limited overlap (Fig. 40A). The dorsal pelage of *A. zambalensis* sp. nov. is a rather bright rusty umber (Fig. 2A), whereas that of *A. sierrae* is either a dark, slightly reddish brown (in the Sierra Madre; Fig. 2C) or a somewhat tawny brown (on Mt. Palali; Fig. 2D). The fore- and hind feet of *A. zambalensis* sp. nov. have almost no dark hairs on the dorsal surface, whereas *A. sierrae* virtually always has at least some dark hairs. The ventral surface of the hind foot of *A. zambalensis* sp. nov. is typically only moderately pigmented and has large plantar pads, whereas *A. sierrae* typically is heavily pigmented and has smaller pads. The hallux of *A. sierrae* is short, reaching only to the bottom of the adjacent plantar pad, whereas that of *A. zambalensis* sp. nov. is long, reaching about to the top of the pad (Fig. 10E,I). The cranium of *A. zambalensis* sp. nov. is larger than that of *A. sierrae*, with a more robust rostrum, broader and more squarish braincase, broader incisive foramina, narrower M^1, less divergent maxillary toothrows, less heavily pitted and perforated palate, and longer postpalatal region. Bivariate plots of postpalatal length vs. breadth of M^1 (Fig. 40B) and rostral depth vs. diastema length (Fig. 40C) taken in combination allow separation of most individuals. The interparietal bones in the two species are variable in shape

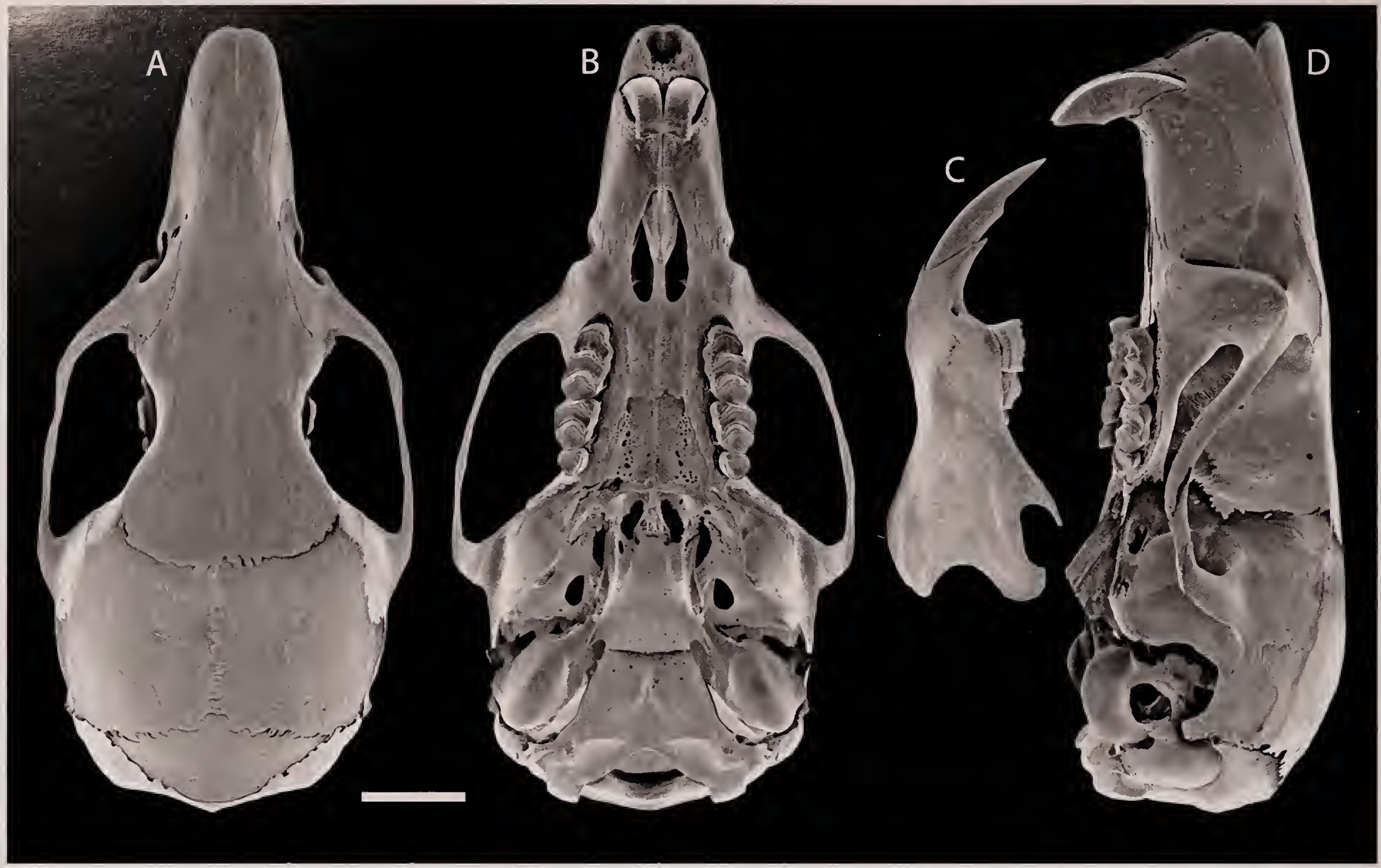


Fig. 34. Dorsal (**A**), ventral (**B**), and lateral (**D**) views of the cranium and lateral view of the mandible (**C**) of *Apomys sierrae* sp. nov. (FMNH 185884, holotype); scale bar = 5 mm.

but usually similar in width. The mandible of *A. zambalensis* sp. nov. is deeper, with a somewhat more robust coronoid process, broader angular process, and broader and slightly less concave posterior margin between the condylar and angular processes. The PCA described above (Fig. 38; Table 14) shows no difference in size (PC1) but overlaps with substantially different averages along PC2, which loads heavily on the dental features, diastema length, and postpalatal length that are individually apparent as differences. These metric differences, combined with the difference in carotid circulatory pattern and clear genetic monophyly, lead us to conclude that these are different species.

Distribution—Specimens referred to this species have a wide distribution, from Palaui Island off the NE tip of Luzon, south through the main mass of the Sierra Madre mountain range in Cagayan Province to Mt. Lataan and the Mungiao Mountains in Quirino Province (Figs. 3, 35). We also refer specimens from Mt. Palali, in the Caraballo Mountains of Nueva Viscaya, to this species because they are genetically and morphologically highly similar, except for having paler pelage. *Apomys sierrae* probably has the broadest geographic range of any species of *Megapomys*, although the ranges of *A. abrae* and *A. datae* are nearly as large. The report by Danielsen et al. (1994) of large *Apomys* tentatively referred to *A. datae* actually refers to this species. The documented elevational range of the species on Luzon is from ca. 475 to 1700 m, one of the greatest among *Apomys* (Fig. 15), but we also recorded it at 153 m on Palaui Island, which has a maximum elevation of about 300 m. The distribution of this species and *A. abrae*, and possibly *A. datae*, might overlap in the area where the Caraballo Mountains and the Central Cordillera come into contact in southwestern Nueva Vizcaya; surveys in that area should produce interesting information about comparative habitat use by these species.

Apomys (*Megapomys*) *magnus* sp. nov.

Holotype—FMNH 183574, adult female collected on 23 February 2005 by Danilo S. Balete, field number DSB 3606. A sample of muscle tissue was removed from the thigh in the field and preserved in ethanol before the specimen was preserved in formaldehyde. In the museum, the skull was removed and cleaned (see Methods). Palate damaged by perforation, pterygoid process broken off and lost from left side; otherwise, in good condition. This specimen will be permanently deposited at the NMP. Measurements appear in Table 12.

Type Locality—Philippines: Luzon Island: Quezon Province: Tayabas Munic.: Barangay Lalo: Mt. Banahaw, Hasa-an, 1250 m; 14°3′44″N, 121°31′8″E (from GPS).

Paratypes (n = 12)—Luzon Island: Quezon Prov.: Tayabas Munic.: Brgy. Lalo: Idoro: Mt. Banahaw, 765 m (FMNH 183569–183572); Tayabas Munic.: Brgy. Lalo: Hasa-an: Mt. Banahaw, 1250 m (FMNH 183573, 183575–183579); Tayabas Munic.: Brgy. Lalo: Mt. Banahaw, 1465 m (FMNH 178395–178396).

Etymology—An adjective from the Latin *magnus*, meaning “large,” in recognition that it is the largest species of *Apomys* currently known.

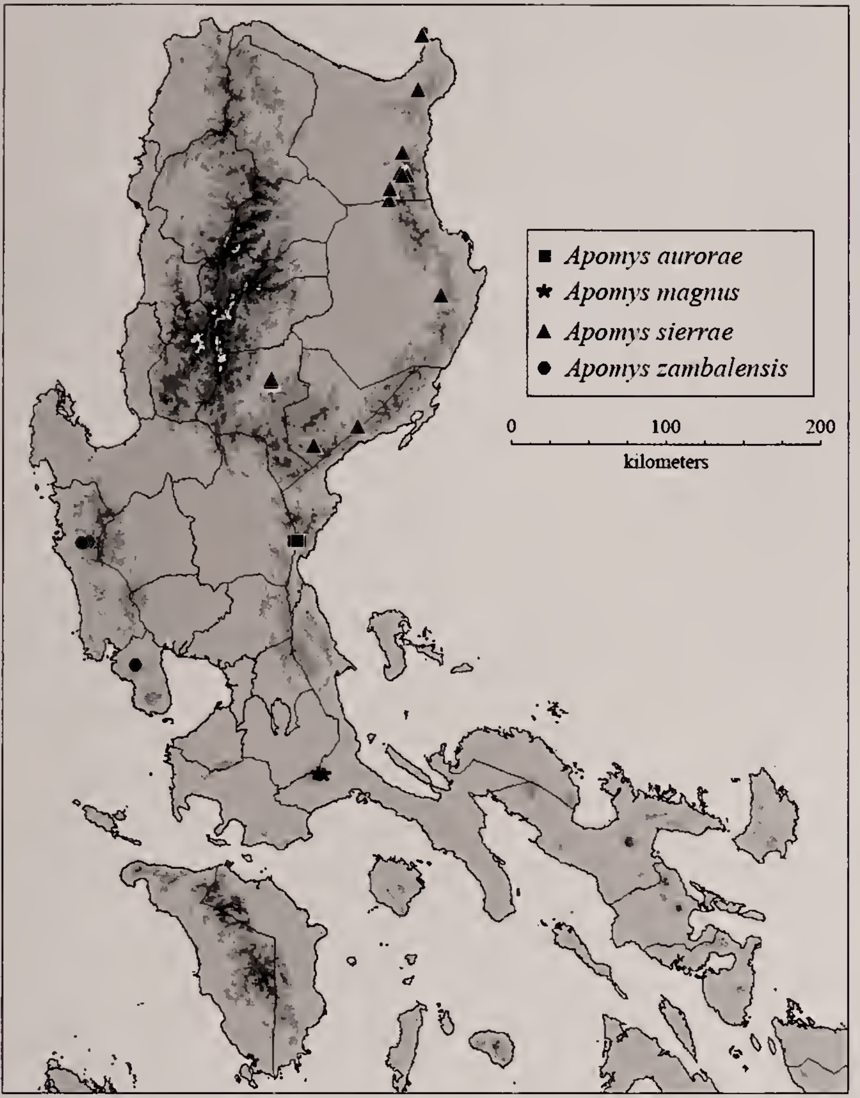


FIG. 35. Map showing the documented distribution of *Apomys aurorae*, *A. magnus*, *A. sierrae*, and *A. zambalensis* spp. nov. See respective species accounts for localities. Shading on land areas, in increasingly dark tones of gray: 0–500 m elevation; 501–1000 m; 1001–1500 m; 1501–2000 m; and white above 2000 m. Provincial boundaries are shown for reference.

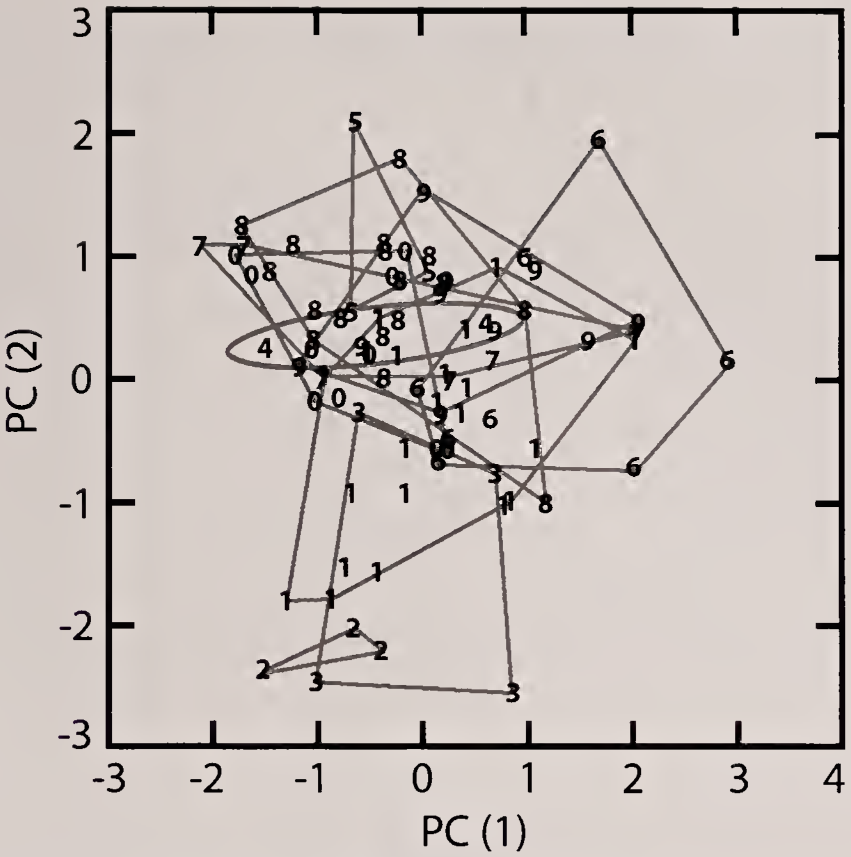


FIG. 36. Results of the principal components analysis of *Apomys sierrae* sp. nov. (see text and Table 13) based on specimens in Tables 9, 11, and 12. 0 = Mt. Cetaceo, Cagayan Province, ca. 1300 m; 1 = Mt. Cetaceo, Cagayan Province, ca. 1500 m; 2 = Palaui Island, Cagayan Province; 3 = Mt. Cagua, Cagayan Province; 4 = Mt. Lataan, Quirino Province; 5 = Mungiao Mtns., Quirino Province; 6 = Mt. Palali, Nueva Vizcaya Province, ca. 800 m; 7 = Mt. Palali, Nueva Vizcaya Province, ca. 1100 m; 8 = Mt. Palali, Nueva Vizcaya Province, ca. 1440 m; 9 = Mt. Palali, Nueva Vizcaya Province, 1700 m.

DIAGNOSIS AND DESCRIPTION—The largest species of *Megapomys*, with HBL averaging about 147 mm, and weight usually 98–108 g; some individuals weighed up to 128 g. The length of the tail is typically 96–99% of the length of HBL. *Apomys magnus* has dorsal fur of moderate length; it is dark brown with conspicuous dark tips, with little evidence of orange or yellow highlights (Fig. 1E). The ventral fur is medium gray at the base, and white at the tips. The tail is unpigmented ventrally and dark brown dorsally. The hind foot is the longest of any *Megapomys*, averaging 39–40 mm; it is broad relative to its length, the plantar pads are of moderate size, and the ventral surface is moderately to heavily pigmented, with the exception of the thenar pad (Fig. 10D). The toes are robust, with the hallux reaching to about the top of the adjacent interdigital plantar pad, and digit 5 reaching nearly to the base of digit 4. The fur on the dorsal surface of the hind foot is white or pale cream. On the forefoot, a stripe of dark hairs extends along the median from the forearm to (or near to) the base of the toes.

The cranium of *A. magnus* (Fig. 41) is the largest among *Megapomys*, averaging about 37.4 mm in basioccipital length and 19.3 in zygomatic width (Table 12). The rostrum is robust and fairly long, and the incisive foramina are unusually long. The braincase is broad and sturdy, and the zygomatic arches are robust and flare to the sides. The maxillary toothrow is long, and M^1 is especially wide. The bony palate is broad and the posterior portion has many small pits and perforations. The postpalatal region is of average length. The basicranial circulation is of the "datae pattern" (Fig. 5B). The interparietal is variable in shape but is usually anteroposteriorly wide. The mandible (Fig. 41C) is robust, with a coronoid process of average length, a broad angular process, and a shallow concave edge between the condylar and angular processes.

COMPARISONS—*Apomys magnus* differs from *A. banahao* in the ways described above for that species, which occurs largely above it in elevation on Mt. Banahaw, but occasionally in sympatry (Fig. 15). In general, *A. banahao* has longer, softer pelage, the hallux is short, the maxillary toothrow is shorter and narrower, the palate is narrower (Fig. 29C), and the bullae lack a foramen for the stapedial artery. Our genetic data show them to be distantly related, confirming them as distinct species.

Apomys magnus differs from *A. sierrae* as described above; *A. sierrae* averages smaller, with little overlap in most external and cranial measurements (Fig. 37), has dorsal fur that is dark brown with rusty reddish tones and ventral fur that is dark gray at the base and pale gray at the tip with an ochraceous wash. The hallux of *A. magnus* is long, and that of *A. sierrae* is short. The crania are usually easily distinguished using a combination of several measurements (Fig. 37B,C), and the stapedial foramen is large and conspicuous in *A. magnus* but absent in *A. sierrae*. The metric differences are apparent in a PCA that includes *A. magnus*, *A. sierrae*, and *A. zambalensis*, discussed in the *A. sierrae* species account (Fig. 38; Table 14).

Apomys magnus differs from *A. aurorae* sp. nov., one of its closest relatives, in being much larger in all external and cranial measurements, often with little overlap (Fig. 42). The dorsal fur of *A. aurorae* sp. nov. (Fig. 2F) is not as dark and has a yellow tint that is absent in *A. magnus* (Fig. 1E), and *A.*

Table 12. Cranial and external measurements (mean ± 1 S.D. and range) of *Apomys sierrae* (part) and *A. magnus.*

	Apomys sierrae			*Apomys magnus*		
	Mt. Palali, 1680–1700 m, Nueva Vizcaya Prov.		**Palaui Island, Cagayan Prov.**	**Mt. Banahaw, 765–1465 m, Quezon Prov. F-holotype**	**Mt. Banahaw, 765–1465 m, Quezon Prov.**	
Measurement	**M (n = 8)**	**F (n = 3)**	**M (n = 3)**	**FMNH 183574**	**M (n = 3)**	**F (n = 6)**
Basioccipital length	35.44 ± 0.96	35.21 ± 0.18	35.14 ± 0.33	37.04	37.06 ± 0.86	37.70 ± 0.49
	33.65–36.34	35.02–35.36	34.76–35.33	—	36.30–38.00	37.04–38.39
Interorbital breadth	6.31 ± 0.20	6.17 ± 0.09	6.16 ± 0.25	6.44	6.55 ± 0.19	6.53 ± 0.19
	6.09–6.68	6.08–6.25	5.90–6.40	—	6.38–6.76	6.25–6.73
Zygomatic breadth	18.76 ± 0.69	18.89 ± 0.10	17.59 ± 0.73	19.40	19.18 ± 0.64	19.38 ± 0.35
	17.65–19.63	18.78–18.95	16.96–18.39	—	18.47–19.73	18.79–19.84
Mastoid breadth	14.67 ± 0.17 (7)	14.43 ± 0.27	14.11 ± 0.23	15.15	14.88 ± 0.27	15.08 ± 0.27
	14.50–14.96	14.20–14.72	13.84–14.26	—	14.70–15.19	14.62–15.37
Nasal length	14.60 ± 0.58	14.54 ± 0.13	14.29 ± 0.55	15.25	15.01 ± 0.37	15.56 ± 0.61
	13.84–15.50	14.39–14.64	13.66–14.63	—	14.59–15.24	14.81–16.35
Incisive foramen length	5.61 ± 0.45	5.63 ± 0.50	5.39 ± 0.29	5.34	5.79 ± 0.18	5.75 ± 0.34
	5.07–6.34	5.10–6.09	5.07–5.63	—	5.65–5.99	5.34–6.12
Rostral depth	7.72 ± 0.26	7.80 ± 0.28	7.52 ± 0.18	7.80	8.11 ± 0.35	8.34 ± 0.30
	7.15–7.96	7.49–8.02	7.33–7.68	—	7.82–8.49	7.80–8.62
Rostral length	15.43 ± 0.30	15.34 ± 0.15	14.94 ± 0.10	16.40	15.64 ± 0.30	16.51 ± 0.53
	14.97–15.86	15.19–15.49	14.83–15.01	—	15.30–15.82	15.91–17.42
Orbitotemporal length	12.31 ± 0.70	12.44 ± 0.33	12.09 ± 0.35	13.09	13.25 ± 0.17	13.13 ± 0.18
	11.33–13.12	12.08–12.73	11.71–12.40	—	13.07–13.41	12.82–13.35
Maxillary toothrow length	7.61 ± 0.17	7.42 ± 0.12	7.07 ± 0.05	8.13	7.95 ± 0.31	8.13 ± 0.19
	7.29–7.80	7.29–7.50	7.03–7.13	—	7.67–8.28	7.78–8.28
Labial palatal breadth at M^1	8.14 ± 0.30	7.99 ± 0.30	7.09 ± 0.13	8.65	8.28 ± 0.29	8.54 ± 0.47
	7.67–8.46	7.65–8.22	6.95–7.20	—	7.96–8.52	7.76–9.03
Diastema length	9.54 ± 0.30	9.35 ± 0.42	9.37 ± 0.21	9.73	9.95 ± 0.20	10.06 ± 0.34
	9.08–10.01	8.86–9.60	9.24–9.62	—	9.75–10.15	9.73–10.50
Postpalatal length	11.43 ± 0.37 (7)	11.14 ± 0.25	11.88 ± 0.14	12.39	12.56 ± 0.38	12.45 ± 0.41
	10.97–11.94	10.85–11.29	11.73–12.01	—	12.19–12.95	12.10–13.21
Lingual palatal breadth at M^3	5.60 ± 0.15	5.40 ± 0.24	4.91 ± 0.31	6.04	5.86 ± 0.31	5.96 ± 0.29
	5.40–5.78	5.13–5.57	4.63–5.24	—	5.64–6.21	5.73–6.51
Braincase height	10.91 ± 0.43 (7)	11.04 ± 0.52	10.48 ± 0.04	11.57	11.15 ± 0.29	11.36 ± 0.25
	10.31–11.57	10.68–11.63	10.44–10.51	—	10.82–11.37	11.06–11.65
Breadth of M^1	1.97 ± 0.05	1.90 ± 0.15	1.78 ± 0.04	2.19	2.09 ± 0.10	2.10 ± 0.07
	1.91–2.05	1.76–2.05	1.73–1.81	—	2.01–2.21	2.01–2.19
Breadth of incisors at tip	2.22 ± 0.07	2.30 ± 0.18	2.18 ± 0.08	2.24	2.41 ± 0.12	2.38 ± 0.12
	2.10–2.33	2.13–2.49	2.09–2.24	—	2.31–2.54	2.24–2.55
Width of zygomatic plate	3.47 ± 0.08	3.57 ± 0.24	3.50 ± 0.08	3.62	3.42 ± 0.04	3.59 ± 0.14
	3.35–3.58	3.29–3.75	3.41–3.55	—	3.40–3.46	3.43–3.81
Length of head and body	143.1 ± 7.3	144.3 ± 2.1	142.0 ± 7.2	137	147.5 ± 0.7 (2)	146.4 ± 8.5 (5)
	132–151	142–146	134–148	—	147–148	137–160
Total length	279.1 ± 13.4	280.7 ± 2.1	279.7 ± 8.5	272	292.5 ± 10.6 (2)	289.2 ± 13.5 (5)
	261–295	279–283	271–288	—	285–300	272–305
Length of tail vertebrae	136.0 ± 9.5	136.3 ± 4.0	137.7 ± 2.1	135	145.0 ± 9.9 (2)	142.8 ± 8.7 (5)
	121–149	134–141	136–140	—	138–152	133–154
Length of hind foot	36.6 ± 1.6	34.7 ± 1.2	35.3 ± 0.6	39	40.3 ± 0.6	38.8 ± 1.2
	35–40	34–36	35–36	—	40–41	37–40
Length of ear	20.0 ± 0.8	19.3 ± 0.6	20.0 ± 1.0	22	22.7 ± 0.6	21.8 ± 0.4 (5)
	19–21	19–20	19–21	—	22–23	21–22
Weight (g)	78.6 ± 7.3	92.0 ± 13.9	83.3 ± 11.0	98	98.7 ± 6.5	108.6 ± 14.4 (5)
	69–90	84–108	72–94	—	92–105	93–128

aurorae sp. nov. lacks the dark tips on dorsal hairs that are conspicuous on *A. magnus*. The ventral surface of the foot is much darker on *A. magnus* than on *A. aurorae* sp. nov., and the hallux of *A. magnus* reaches to about the top of the adjacent interdigital plantar pad, whereas that of *A. aurorae* sp. nov. reaches only to the base of the pad (Fig. 10G). Bivariate plots of basioccipital length and interorbital breadth, and of nasal length and rostral depth, show no overlap between these species (Fig. 42B,C). The interparietal of *A. magnus* is variable in shape but usually somewhat wider anteroposteriorly than that of *A. aurorae* sp. nov. As described in the species account for *A. sacobianus*, a PCA of that species plus *A. aurorae* sp. nov., *A. magnus*, and *A. zambalensis* sp. nov. showed complete separation of *A. magnus* and *A. aurorae* sp. nov. on a plot of PC1 and PC2, primarily reflecting their consistent difference in overall size (Fig. 23; Table 7). This difference, combined with their genetic monophyly, leads us to treat them as different species.

Apomys magnus differs from *A. zambalensis* sp. nov., another close relative, in having longer dorsal fur with black tips; *A. zambalensis* sp. nov. has fur that is a brighter, rusty orange with only barely evident black tips. The ventral fur of *A. magnus* is gray at the base and nearly white at the tips; that of *A. zambalensis* sp. nov. is a paler gray at the base and white

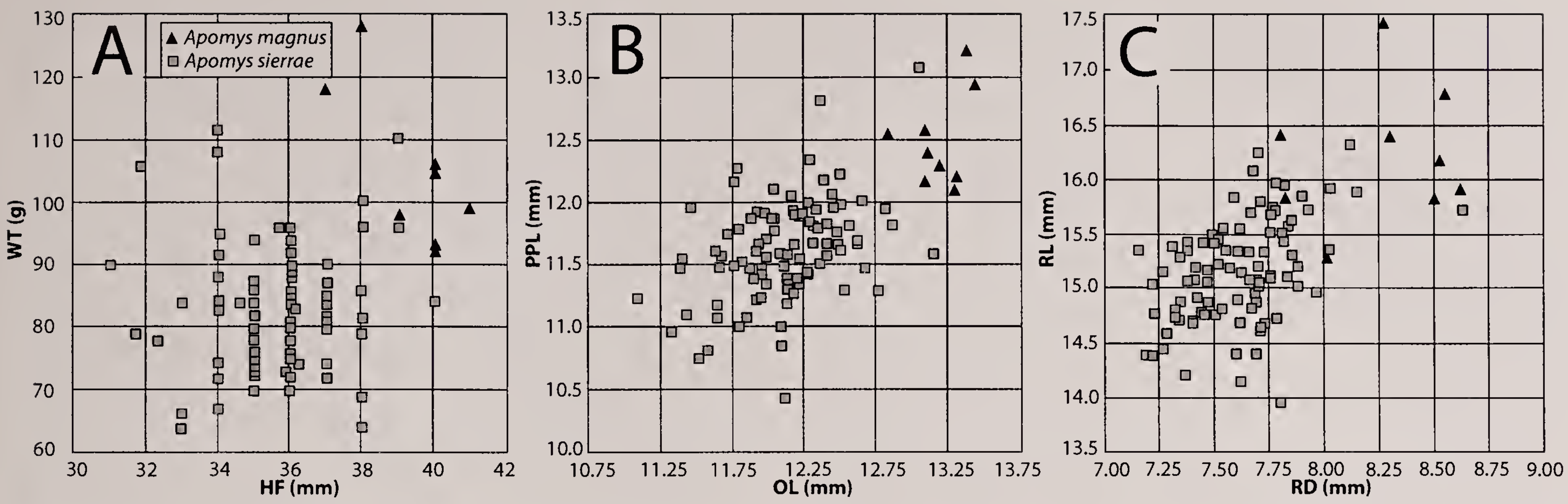


FIG. 37. Bivariate plots of measurements comparing *Apomys sierrae* and *A. magnus* spp. nov. (**A**) Length of hind foot (HF) and weight (WT). (**B**) Orbitotemporal length (OL) and postpalatal length (PPL). (**C**) Rostral depth (RD) and rostral length (RL).

at the tips with an ochraceous wash. The hind feet are similar, but those of *A. zambalensis* sp. nov. are slightly smaller (39–40 vs. 37–38 mm) and less heavily pigmented (Fig. 10I). A plot of weight vs. total length (Fig. 43A) shows that *A. magnus* is usually longer and heavier, but there is overlap. A plot of the width of M^1 vs. breadth of incisors at the tip shows no overlap (Fig. 43B), and length of the maxillary toothrow vs. labial palatal breadth at M^1 shows little overlap (Fig. 43C); *A. magnus* is the larger in all of these measures. These metric differences are apparent in a PCA that includes *A. magnus*, *A. sierrae*, and *A. zambalensis*, discussed in the *A. sierrae* species account, which shows no overlap between *A. magnus* and *A. zambalensis* sp. nov. on the plot of PC1 vs. PC2 (Fig. 38; Table 14). The combination of discrete morphological features, multivariate morphometric differences, and genetic monophyly lead us to consider these to be clearly distinct species.

DISTRIBUTION—Our elevational transect on Mt. Banahaw documented this species from 765 to 1465 m in lowland and montane rainforest (Figs. 15, 35). Extensive trapping at 620 m failed to detect this species, and we doubt that it occurs below about 700 m. We suspect that it occurs on Mt. Banahaw and the adjacent Mt. San Cristobal (in Laguna and Quezon provinces) from about 700 to about 1465 m elevation, in any forested area. Above about 1465 m, we captured large numbers of *A. banahao*, so we expect *A. magnus* to be absent from high-elevation areas. Mts. Banahaw and San Cristobal sit on a flat, low-elevation (below 300 m) plain, with scattered peaks, largely below 1000 m, within 50 km in any direction. We predict that this species will not be found in any other areas, but surveys of the peaks in the general vicinity (Batangas, Cavite, Laguna, and southern Quezon provinces) would be worthwhile, especially at elevations above 700 m.

Apomys (*Megapomys*) *aurorae* sp. nov.

HOLOTYPE—FMNH 190812, adult male collected on 15 June 2006 by Phillip A. Alviola, field number PAA 864. A sample of muscle tissue was removed from the thigh in the field and preserved in ethanol before preserving the specimen in formaldehyde. In the museum, the skull was removed and cleaned (see Methods). All parts are in good condition. This specimen will be permanently deposited at the NMP. Measurements appear in Table 15.

TYPE LOCALITY—Philippines: Luzon Id: Aurora Province: Dingalan Munic.: 2 km S, 2 km W Mingan peak, 1305 m, 15.46456°N, 121.38421°E (from GPS).

PARATYPES (n = 98)—Luzon Island: Aurora Prov.: Dingalan Munic.: 2.25 km S, 3.25 km W Mingan peak, 733 m (FMNH 190933–190935); Dingalan Munic.: 2.1 km S, 2.9 km W Mingan peak, 902 m (FMNH 190825, 190918–190932); Dingalan Munic.: 1.9 km S, 2.5 km W Mingan peak, 1074 m (FMNH 190826–190832, 190925, 190929); Dingalan Munic.: 2 km S, 2 km W Mingan peak, 1305 m (FMNH 190810, 190811, 190813–190824, 190910–190917, 191067–191076); Dingalan Munic.: 1.8 km S, 1.6 km W Mingan peak, 1476 m (FMNH 190794–190809, 190887–190909, 191066); Dingalan Munic.: 1.7 km S, 1.3 km W Mingan peak, 1540 m (FMNH 190953); Dingalan

TABLE 13. Character loadings, eigenvalues, and percent variance explained on the first four components of a principal components analysis of log-transformed measurements of adult *Apomys sierrae* (see Fig. 36 and Methods).

	Principal component			
Variable	1	2	3	4
Basioccipital length	0.824	−0.266	0.099	−0.250
Interorbital breadth	0.567	−0.325	0.207	0.272
Zygomatic breadth	0.723	0.263	0.064	0.299
Mastoid breadth	0.633	0.120	0.219	0.383
Nasal length	0.705	−0.009	−0.338	−0.171
Incisive foramen length	0.460	0.010	−0.137	−0.485
Rostral depth	0.719	0.086	−0.217	−0.010
Rostral length	0.767	−0.158	−0.289	0.015
Orbitotemporal length	0.672	−0.100	0.002	−0.380
Maxillary toothrow length	−0.009	0.701	0.328	−0.395
Labial palatal breadth at M^1	0.635	0.675	−0.123	0.078
Diastema length	0.696	−0.434	−0.110	0.126
Postpalatal length	0.556	−0.478	0.203	−0.305
Lingual palatal breadth at M^3	0.530	0.389	−0.178	0.421
Braincase height	0.290	−0.004	0.697	0.046
Breadth of M^1	0.127	0.782	−0.026	−0.224
Breadth of incisors at tip	0.391	0.029	0.595	−0.007
Width of zygomatic plate	0.335	0.288	0.000	0.034
Eigenvalue	6.032	2.514	1.416	1.283
Percent variance explained	33.51	13.96	7.87	7.13

Table 14. Character loadings, eigenvalues, and percent variance explained on the first four components of a principal components analysis of log-transformed measurements of adult *Apomys magnus*, *A. sierrae*, and *A. zambalensis* (see Fig. 38 and Methods).

Variable	Principal component			
	1	2	3	4
Basioccipital length	0.866	−0.308	−0.228	−0.071
Interorbital breadth	0.498	0.244	0.543	−0.227
Zygomatic breadth	0.785	0.213	0.203	0.071
Mastoid breadth	0.695	0.249	0.140	−0.101
Nasal length	0.745	0.032	0.170	0.205
Incisive foramen length	0.526	−0.050	−0.026	0.086
Rostral depth	0.771	−0.188	−0.022	0.167
Rostral length	0.784	−0.244	0.169	0.192
Orbitotemporal length	0.753	−0.094	−0.182	0.024
Maxillary toothrow length	0.454	0.498	−0.589	−0.075
Labial palatal breadth at M^1	0.701	0.511	0.012	0.198
Diastema length	0.667	−0.582	0.092	−0.007
Postpalatal length	0.553	−0.606	−0.311	−0.188
Lingual palatal breadth at M^3	0.588	−0.025	0.301	0.052
Braincase height	0.501	0.140	0.019	−0.542
Breadth of M^1	0.313	0.820	−0.116	0.077
Breadth of incisors at tip	0.533	0.085	−0.222	−0.478
Width of zygomatic plate	0.298	−0.010	−0.280	0.561
Eigenvalue	7.220	2.284	1.184	1.113
Percent variance explained	40.11	12.69	6.58	6.18

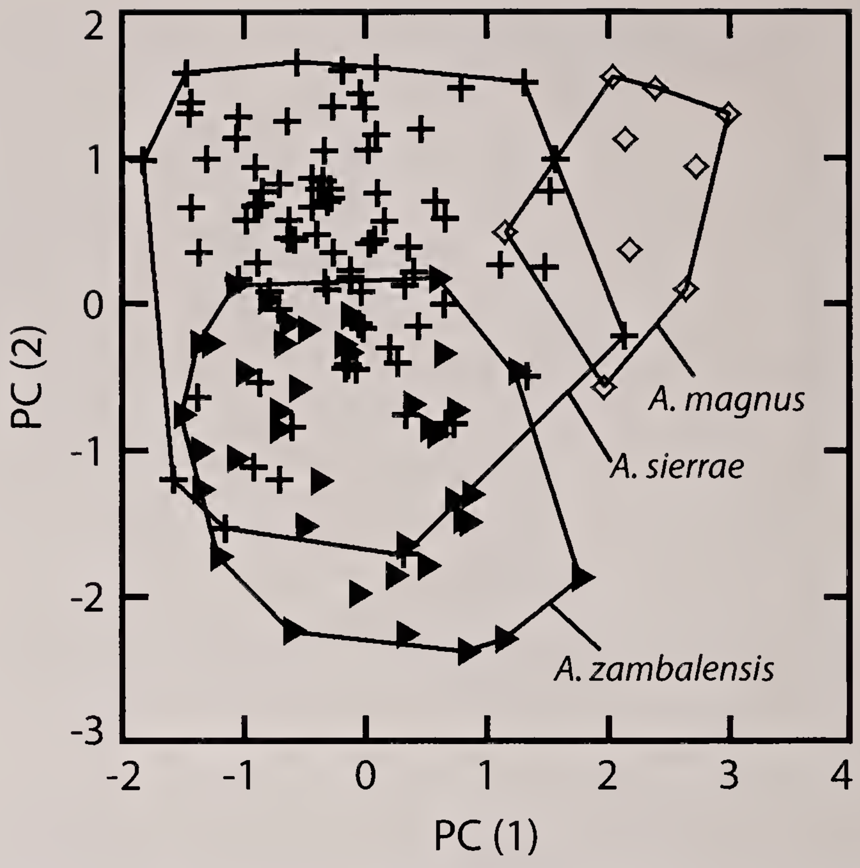


Fig. 38. Results of the principal components analysis of *Apomys sierrae*, *A. magnus*, and *A. zambalensis* spp. nov. (see text and Table 14) based on specimens in Tables 9, 11, 12, and 15.

Munic.: 1.8 km S, 1.0 km W Mingan peak, 1677 m (fmnh 190846).

Etymology—From the name of the province (Aurora) where this species was captured; used as a noun in the genitive case.

Diagnosis and Description—One of the smaller species of *Megapomys*, although averaging only slightly larger than *A. minganensis*, *A. brownorum*, and *A. abrae* in most measurements (Tables 2, 3, 9). The dorsal pelage of *A. aurorae* is rich, rusty reddish-brown, with medium-gray underfur (Fig. 2F). The ventral pelage is somewhat paler at the base, with the tips either white or white with a pale ochraceous wash. The brown pelage extends only a short distance onto the forearms and lower hind legs, but scattered dark hairs are sometimes present on the upper surface of the forefeet and hind feet. The ventral surface of the hind feet is usually moderately darkly pigmented, often including the pads, and the hallux is short, reaching only to about the bottom of the adjacent interdigital plantar pad (Fig. 10G). The tail is sharply bicolored and long, averaging 98–100% of the length of the head and body. The ventral surface of the tail is usually white, but some individuals have scattered dark hairs and darkly pigmented scales.

The cranium (Fig. 44) has a somewhat globose braincase that is less elongate than most species, a moderately short and comparatively slender rostrum, a short diastema, and a short postpalatal region. The molar toothrows are of average length and width and diverge posteriorly, and the bony palate is moderately broad. The stapedial foramen in the bulla for the carotid artery is present in all individuals (the "datae pattern"; Fig. 5). The interparietal is variable in shape, but usually is moderately wide anteroposteriorly. The mandible (Fig. 44C) is of average depth with a relatively long and posteriorly curved coronoid process. The angular process is broad and has a blunt tip.

Comparisons—*Apomys aurorae* differs from *A. minganensis* as described above; *A. minganensis* is darker dorsally and ventrally, always has a tail with scattered dark hairs and pigment ventrally, and has dark hair on the entire dorsal surface of the hind feet. The hallux of *A. aurorae* is short, reaching only to about the bottom of the adjacent interdigital pad, whereas that of *A. minganensis* is long, reaching to about the top of the pad. There is no overlap between these species in rostral depth, orbital length, or length of the maxillary toothrow, and there is little overlap in lingual breadth of the palate at M^3 (Fig. 31C). As described above, a PCA of craniodental measurements that included *A. aurorae, A. minganensis*, and *A. sierrae* (Fig. 33; Table 10) showed no overlap in a plot of PC1 vs. PC2, with most of the differences reflecting the features shown in Figures 31B and C. On the basis of the qualitative and quantitative differences and the genetic evidence of monophyly of these two populations, we conclude that they represent distinct species.

Apomys aurorae differs from *A. sierrae* only in subtle ways, as described above. They are most easily distinguished by the presence of a foramen for the stapedial artery in the bullae of *A. aurorae* (the "datae pattern"; Fig. 5B) and its absence in *A. sierrae* (the "abrae pattern"; Fig. 5A). A PCA of craniodental measurements (Fig. 33; Table 10), discussed above, showed complete overlap on the two interpretable components, but the difference in the stapedial foramen and the genetic evidence of monophyly leads us to view these as distinct species.

Apomys aurorae differs from *A. magnus* in being consistently smaller in all external and cranial measurements, so it is easily distinguished (Fig. 42). The carotid circulation pattern is the same (the "datae pattern"; Fig. 5B) in these two species. The dorsal fur of *A. aurorae* (Fig. 2F) is not as dark and has a yellow tint that is absent in *A. magnus* (Fig. 1E), and *A. aurorae* lacks the dark tips on dorsal hairs that are conspicuous on *A. magnus*. *Apomys magnus* has few or no dark hairs on the dorsal surface of the hind foot, but some individuals of *A. aurorae* have scattered dark hairs. Further-

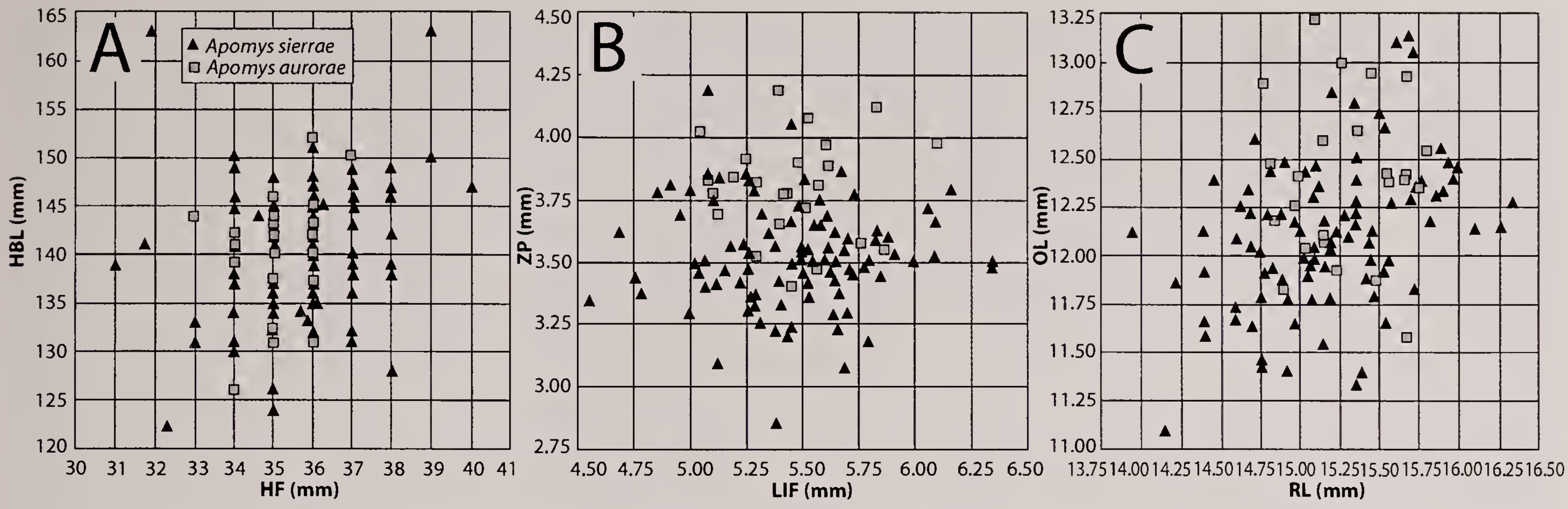


Fig. 39. Bivariate plots of measurements comparing *Apomys sierrae* and *A. aurorae* spp. nov. (**A**) Length of hind foot (HF) and length of head and body (HBL). (**B**) Length of incisive foramen (LIF) and width of zygomatic plate (ZP). (**C**) Rostral length (RL) and orbitotemporal length (OL).

more, the ventral surface of the foot is much darker on *A. magnus* than on *A. aurorae*, and the hallux of *A. aurorae* is short, reaching only to the bottom of the adjacent plantar pad (Fig. 10G), whereas that of *A. magnus* is long, reaching to about the top of the pad (Fig. 10D). Bivariate plots of basioccipital length and interorbital breadth, and of nasal length and rostral depth, show no overlap between these species (Fig. 42B,C). The interparietal of *A. aurorae* is usually somewhat smaller than that of *A. magnus*. A PCA of craniodental measurements (Fig. 23; Table 7), discussed above, showed no overlap on the first component, which reinforces the consistent difference in size. Combined with the qualitative features summarized here and the genetic evidence of monophyly (Fig. 7), we conclude that these are distinct species.

Apomys aurorae is similar in size to *A. zambalensis* sp. nov. in some respects, but other features differ with little overlap. The dorsal pelage of *A. aurorae* is darker brown (Fig. 2F), whereas that of *A. zambalensis* sp. nov. is bright rusty orange (Fig. 2A); the ventral fur of *A. zambalensis* sp. nov. has a moderate to heavy ochraceous wash, whereas *A. aurorae* has less of the ochraceous wash. The hind foot of *A. zambalensis* sp. nov. is usually longer (Fig. 45A) and the ventral surface less heavily pigmented, with a longer hallux than that of *A. aurorae* (Fig. 10G,I). The cranium of *A. zambalensis* sp. nov. is usually larger overall, with a deeper rostrum and longer postpalatal region (Fig. 45B) and narrower M^1, although there is some overlap. A PCA of craniodental measurements (Fig. 23; Table 7), discussed above, showed complete overlap on the first component, which reinforces the overall similarity in size. On the second component, which loaded heavily (and positively) on diastema length and postpalatal length and (negatively) on interorbital breadth, palatal breadth at M^1, and width of the zygomatic plate, the overlap between these species was limited. Combined with the qualitative differences summarized here and the genetic evidence of monophyly (Fig. 7), we conclude that these are closely related but distinct species.

Distribution—Our elevational transect of the Mingan Mountains documented this species from 733 to 1677 m (Figs. 3, 15, 35; Balete et al., this volume). It was the most abundant species along the transect from 902 to 1476 m. At the low end of the transect, we captured none at our 559-m sampling area, and at the high end, we captured only one at

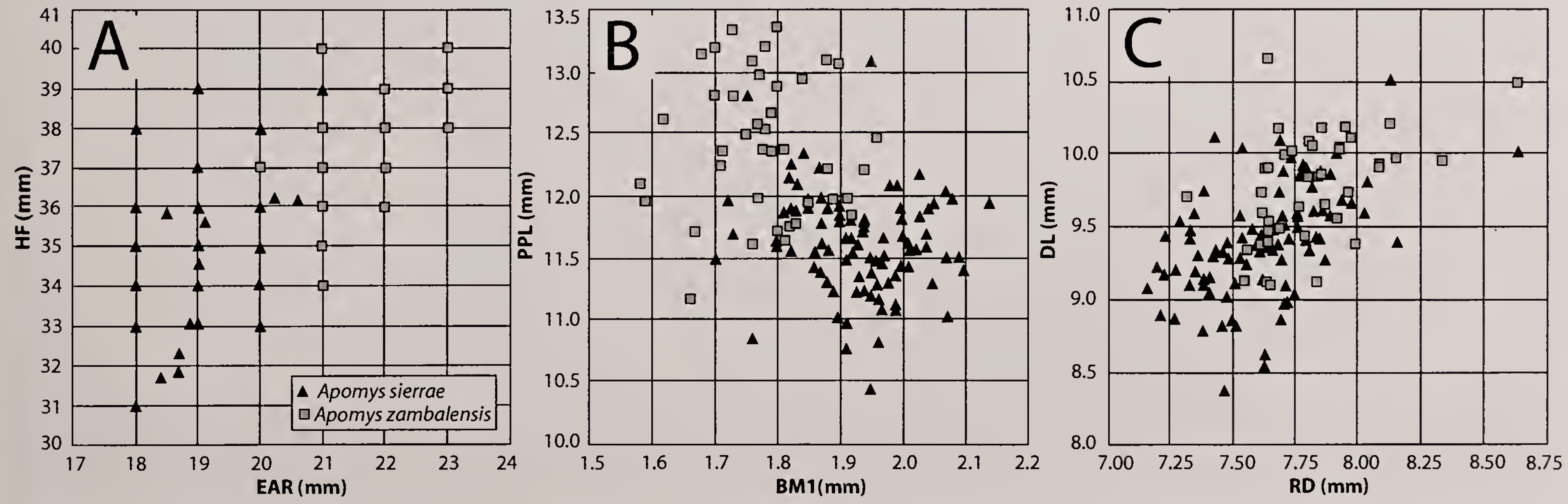


Fig. 40. Bivariate plots of measurements comparing *Apomys sierrae* and *A. zambalensis* spp. nov. (**A**) Length of ear (EAR) and length of hind foot (HF). (**B**) Breadth of M^1 (BM^1) and postpalatal length (PPL). (**C**) Rostral depth (RD) and diastema length (DL).

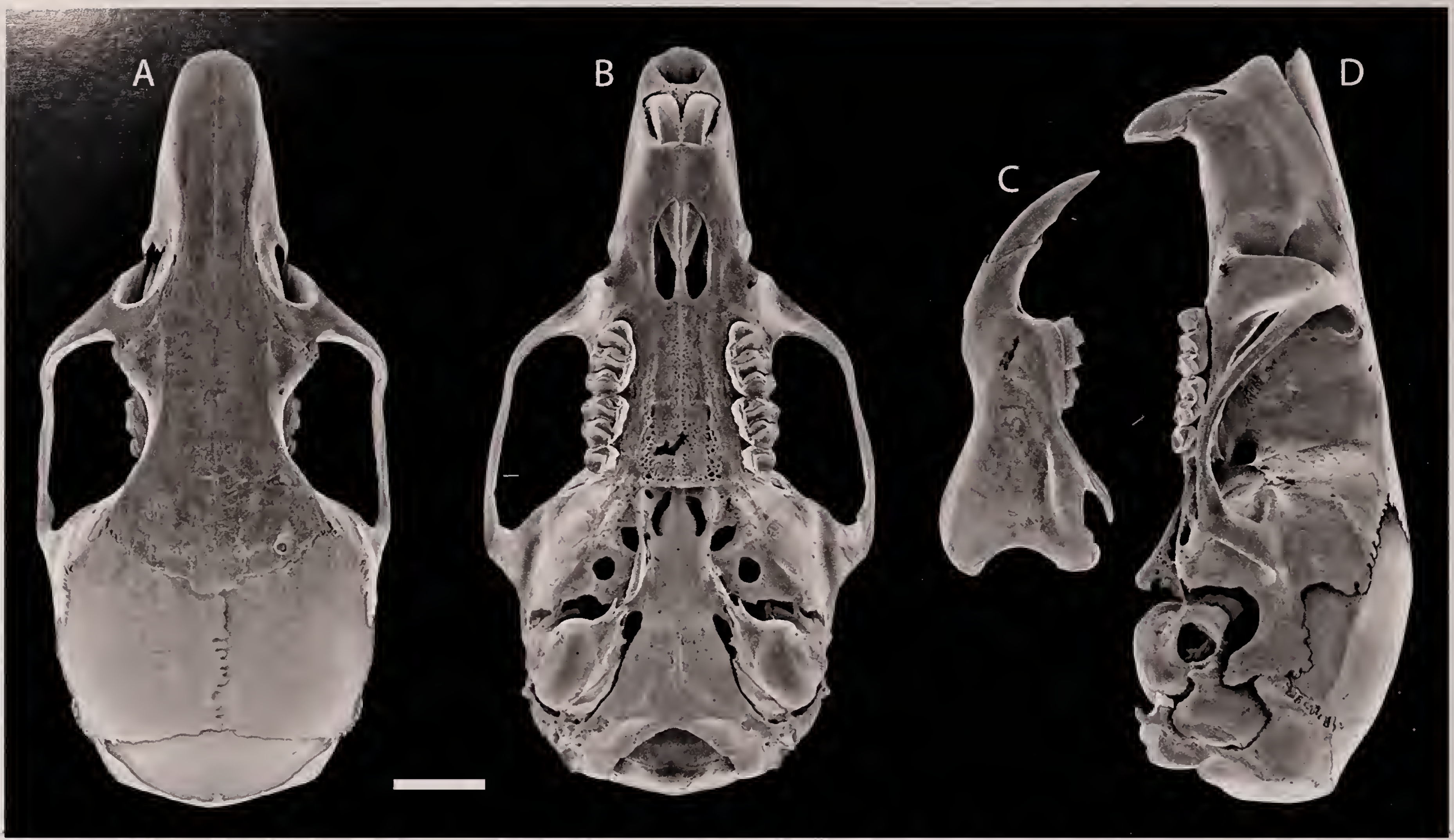


Fig. 41. Dorsal (**A**), ventral (**B**), and lateral (**D**) views of the cranium and lateral view of the mandible (**C**) of *Apomys magnus* sp. nov. (FMNH 183574, holotype); scale bar = 5 mm.

1540 m (plus 8 *A. minganensis*), one at 1677 m (plus 24 *A. minganensis*), and none at 1681 or 1785 m (where *A. minganensis* was common). We infer that this species may be expected throughout the Mingan Mountains from about 700 to 1675 m, with no *Megapomys* below 700 m and only *A. minganensis* above about 1700 m.

No specimens of *A. aurorae* are currently available other than from our transect (Fig. 35), so the extent of its distribution is uncertain. The Mingan Mountains lie in the central portion of Aurora Province and the adjacent area of Nueva Ecija Province (Fig. 3). Areas of low elevation lie to the north and to the south of the Mingan Mountains, with passes at ca. 250 and 300 m, respectively, which is well below the lower elevational limit currently documented for this species; thus, the Mingan Mountains appear to function as a habitat island for this species. There are specimens of *A. sierrae* from northern Aurora Province and from Nueva Vizcaya, just to the north of the Mingan Mountains (Fig. 35), so we predict that *A. aurorae* will not be found to the north of the Mingan Mountains (i.e., not north of the road that goes from Bongabon, Nueva Ecija, to Baler, Aurora). Beyond the low pass to the south (south of Gabaldon, Nueva Ecija, and Dingalan, Aurora), there are no known specimens of *Megapomys* from a long, rugged section of the southern Sierra Madre that has Mt. Irid and Mt. Angilo as the high points (in Rizal and nearby Quezon provinces; Fig. 3). Since

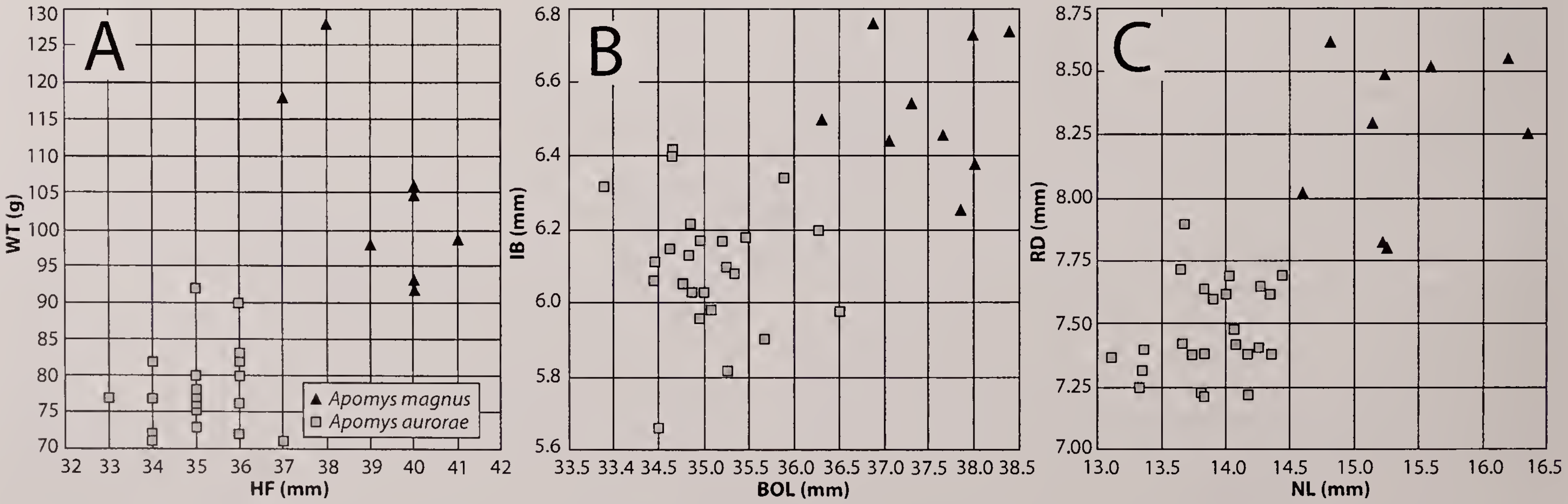


Fig. 42. Bivariate plots of measurements comparing *Apomys magnus* and *A. aurorae* spp. nov. (**A**) Length of hind foot (HF) and weight (WT). (**B**) Basioccipital length (BOL) and interorbital breadth (IB). (**C**) Nasal length (NL) and rostral depth (RD).

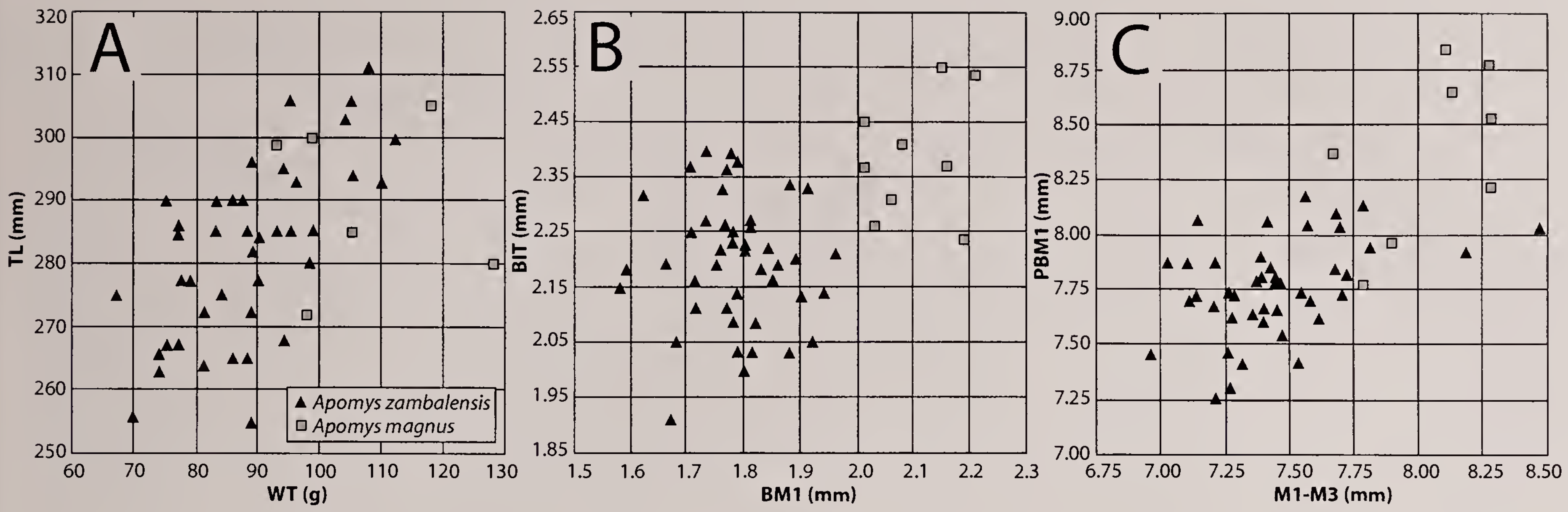


FIG. 43. Bivariate plots of measurements comparing *Apomys magnus* and *A. zambalensis* spp. nov. (**A**) Weight (WT) and total length (TL). (**B**) Breadth of M^1 (BM^1) and breadth of incisors at tip (BIT). (**C**) Length of maxillary molariform toothrow (M^1–M^3) and labial palatal breadth at M^1 (PBM^1).

the peaks in this region reach well over 1000 m, *Megapomys* should be present and should be sought to determine whether *A. aurorae* occurs there, or whether yet another, currently unknown species of *Megapomys* is present.

Apomys (*Megapomys*) *zambalensis* sp. nov.

HOLOTYPE—FMNH 183420, adult female collected on 25 March 2005 by Lawrence R. Heaney, field number LRH 7339. A sample of muscle tissue was removed from the thigh in the field and preserved in ethanol before preserving the specimen in formaldehyde. In the museum, the skull was removed and cleaned (see Methods). All parts are in good condition. This specimen will be permanently deposited at the NMP. Measurements in Table 15.

TYPE LOCALITY—Philippines: Luzon Id.: Bataan Province: 0.1 km N Mt. Natib peak, 1150 m, 14.71513°N, 120.39892°E (GPS reading).

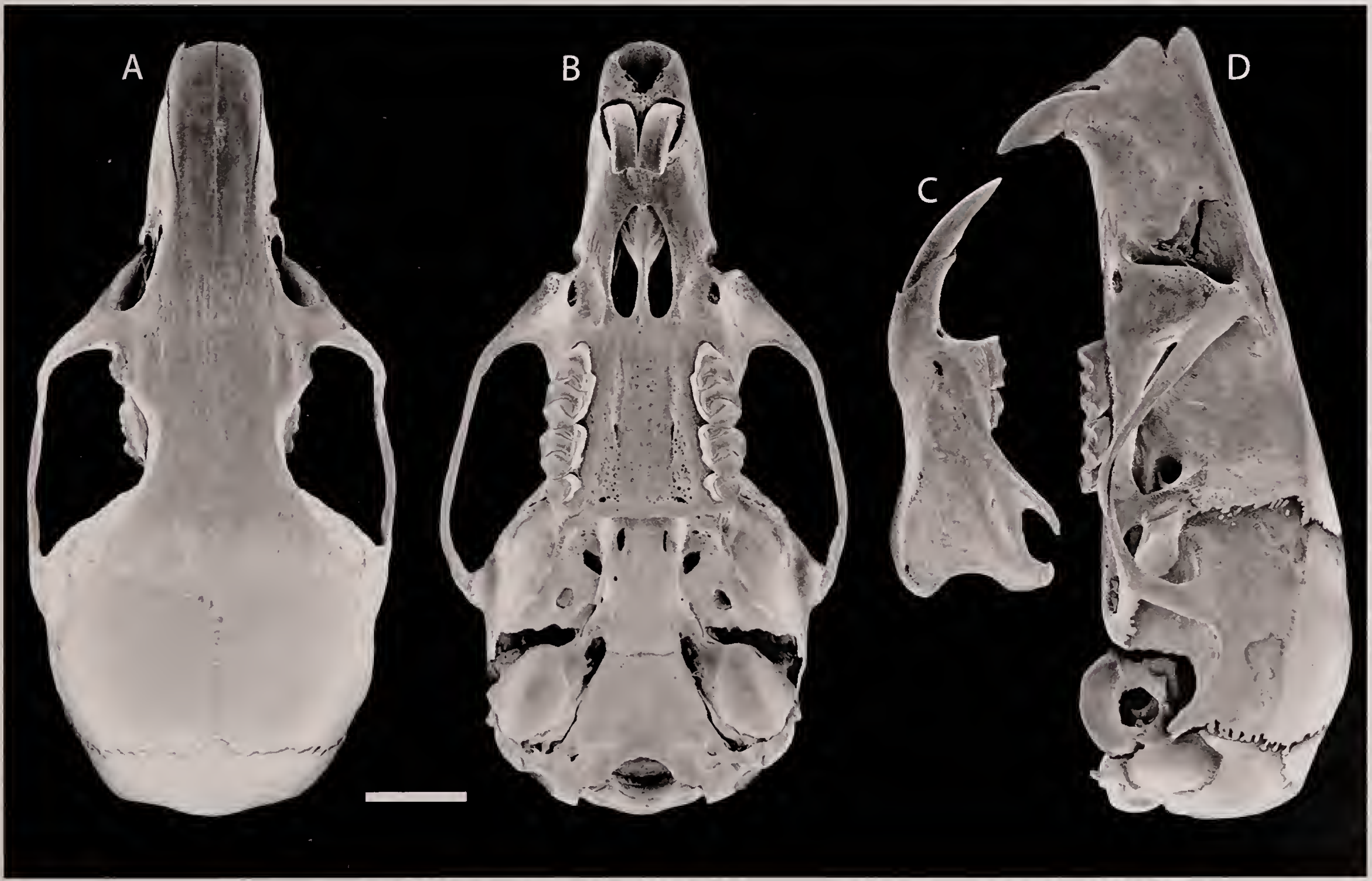


FIG. 44. Dorsal (**A**), ventral (**B**), and lateral (**D**) views of the cranium and lateral view of the mandible (**C**) of *Apomys aurorae* sp. nov. (FMNH 190812, holotype); scale bar = 5 mm.

TABLE 15. Cranial and external measurements (mean ± 1 S.D. and range) of *Apomys aurorae* and *A. zambalensis.*

	Apomys aurorae			*Apomys zambalensis*				
	Mingan Mtns., 733–1677 m, Aurora Prov.			Mt. Natib, Bataan Prov.			Mt. Tapulao, 860–1690 m, Zambales Prov.	
Measurement	M-holotype FMNH 190812	M (n = 12)	F (n = 12)	F-holotype FMNH 183420	M (n = 12)	F (n = 13)	M (n = 10)	F (n = 8)
Basioccipital length	35.25	35.23 ± 0.49	34.87 ± 0.65	36.99	35.78 ± 1.16	36.04 ± 0.99	35.43 ± 0.95	35.46 ± 1.18
	—	34.61–36.25	33.88–36.51	—	34.61–38.14	34.28–37.12	34.30–37.25	33.51–37.43
Interorbital breadth	5.81	6.08 ± 0.15	6.12 ± 0.20	6.29	5.92 ± 0.13	5.82 ± 0.20	6.14 ± 0.20	5.94 ± 0.20
	—	5.81–6.34	5.66–6.42	—	5.70–6.09	5.51–6.29	5.81–6.54	5.67–6.28
Zygomatic breadth	18.15	18.09 ± 0.33 (11)	18.13 ± 0.57	18.13	17.95 ± 0.43	18.15 ± 0.58	18.30 ± 0.52	18.27 ± 0.42
	—	17.61–18.53	17.34–19.27	—	17.29–18.76	17.20–19.21	17.49–19.37	17.58–18.80
Mastoid breadth	14.40	14.25 ± 0.17	14.35 ± 0.20	14.74	14.35 ± 0.35	14.40 ± 0.33	14.10 ± 0.23	14.13 ± 0.39
	—	13.98–14.53	14.11–14.73	—	13.78–15.00	13.89–14.75	13.82–14.38	13.74–14.73
Nasal length	14.18	14.03 ± 0.31	13.76 ± 0.34	14.26	14.11 ± 0.45	14.22 ± 0.41	14.29 ± 0.46	14.27 ± 0.52
	—	13.33–14.36	13.11–14.44	—	13.34–14.97	13.67–15.06	13.70–15.08	13.42–14.89
Incisive foramen length	5.57	5.49 ± 0.31	5.41 ± 0.21	5.67	5.45 ± 0.29	5.36 ± 0.31	5.30 ± 0.29	5.63 ± 0.40
	—	5.04–6.10	5.08–5.83	—	4.81–5.83	4.89–5.87	4.88–5.77	5.30–6.30
Rostral depth	7.38	7.40 ± 0.14	7.53 ± 0.18	7.81	7.72 ± 0.16	7.80 ± 0.23	7.90 ± 0.29	7.81 ± 0.24
	—	7.22–7.65	7.22–7.72	—	7.54–8.08	7.31–8.14	7.64–8.63	7.61–8.32
Rostral length	15.00	15.22 ± 0.36	15.40 ± 0.27	15.64	15.41 ± 0.58	15.31 ± 0.59	15.69 ± 0.43	15.51 ± 0.64
	—	14.77–15.74	14.97–15.79	—	14.74–16.35	14.42–16.19	15.17–16.70	14.77–16.34
Orbitotemporal length	12.41	12.47 ± 0.48	12.31 ± 0.33	12.36	12.20 ± 0.46	12.08 ± 0.41	12.40 ± 0.27	12.54 ± 0.52
	—	11.57–13.21	11.86–12.92	—	11.58-13.22	11.03–12.75	11.95–12.70	11.51–13.31
Maxillary toothrow length	7.42	7.52 ± 0.16	7.39 ± 0.25	7.41	7.46 ± 0.24	7.53 ± 0.40	7.38 ± 0.19	7.40 ± 0.16
	—	7.29–7.79	7.09–8.01	—	7.10–7.81	7.11–8.47	6.96–7.68	7.13–7.57
Labial palatal breadth at M^1	8.04	7.88 ± 0.19	7.84 ± 0.21	8.05	7.78 ± 0.20	7.81 ± 0.26	7.71 ± 0.12	7.68 ± 0.28
	—	7.60–8.21	7.61–8.23	—	7.41–8.13	7.30–8.09	7.45–7.84	7.25–8.17
Diastema length	9.37	9.43 ± 0.23	9.42 ± 0.37	10.05	9.74 ± 0.42	9.77 ± 0.32	9.78 ± 0.44	9.80 ± 0.32
	—	9.15–9.86	9.07–10.30	—	9.14–10.66	9.12–10.18	9.11–10.49	9.39–10.19
Postpalatal length	11.52	11.62 ± 0.31	11.43 ± 0.32	13.20	12.59 ± 0.52	12.62 ± 0.48	12.18 ± 0.49 (8)	12.04 ± 0.59
	—	11.26–12.17	10.83–11.83	—	11.94–13.38	11.72–13.20	11.71–13.20	11.17–13.08
Lingual palatal breadth at M^3	5.44	5.41 ± 0.21	5.59 ± 0.19	6.23	5.49 ± 0.26	5.61 ± 0.31	5.44 ± 0.30 (9)	5.62 ± 0.19
	—	5.16–5.94	5.27–5.84	—	5.16–5.93	5.19–6.23	4.98–5.95	5.32–5.97
Braincase height	10.65	10.78 ± 0.40	10.78 ± 0.37	11.22	10.82 ± 0.31	10.84 ± 0.20	10.86 ± 0.30	10.72 ± 0.28
	—	10.03–11.29	10.21–11.50	—	10.23–11.26	10.45–11.22	10.46–11.46	10.31–11.19
Breadth of M^1	1.96	1.95 ± 0.07	1.88 ± 0.05	1.70	1.82 ± 0.07	1.76 ± 0.09	1.81 ± 0.09	1.74 ± 0.10
	—	1.87–2.06	1.82–1.96	—	1.73–1.94	1.62–1.96	1.59–1.92	1.58–1.91
Breadth of incisors at tip	2.36	2.20 ± 0.10	2.14 ± 0.10	2.25	2.22 ± 0.10	2.22 ± 0.14	2.15 ± 0.10	2.19 ± 0.10
	—	2.08–2.36	1.96–2.28	—	2.11–2.40	1.91–2.38	2.00–2.27	2.03–2.33
Width of zygomatic plate	3.81	3.80 ± 0.16	3.80 ± 0.25	3.34	3.56 ± 0.24	3.53 ± 0.20	3.52 ± 0.21	3.64 ± 0.35
	—	3.55–4.07	3.40–4.19	—	3.19–3.87	3.20–3.91	3.19–3.81	3.18–4.17
Length of head and body	145	143.5 ± 4.7 (11)	136.9 ± 6.0 (11)	158	145.3 ± 6.7	147.7 ± 9.0 (12)	139.6 ± 6.5 (9)	139.6 ± 6.9 (7)
	—	137–152	126–144	—	134–156	129–163	131–148	127–150
Total length	287	285.2 ± 8.2 (11)	272.7 ± 9.0 (11)	306	283.9 ± 13.7	286.9 ± 15.8 (12)	278.9 ± 11.6 (9)	277.9 ± 10.3 (7)
	—	273–295	262–285	—	263–306	264–311	256–290	265–295
Length of tail vertebrae	142	141.7 ± 5.3 (11)	135.5 ± 5.7	148	138.7 ± 9.8	139.3 ± 8.8 (12)	141.2 ± 9.2	138.3 ± 5.3 (7)
	—	136–153	129–147	—	125–158	123–149	125–158	129–145
Length of hind foot	36	35.6 ± 0.8	34.7 ± 0.9	39	38.1 ± 1.3	38.0 ± 0.9	37.1 ± 1.2	36.8 ± 0.9
	—	34–37	33–36	—	36–40	37–39	36–39	35–38
Length of ear	20	19.8 ± 0.8	20.0 ± 0.7 (9)	22	21.8 ± 0.9	21.9 ± 0.8 (11)	21.1 ± 0.6 (9)	21.6 ± 0.5 (7)
	—	18–21	19–21	—	21–23	21–23	20–22	21–22
Weight (g)	80	81.2 ± 5.9 (11)	73.8 ± 6.3 (11)	105	88.7 ± 12.9	93.4 ± 10.6	84.2 ± 11.1	87.4 ± 9.1
	—	71–92	58–83	—	74–112	74–108	70–105	67–95

PARATYPES (n = 231)—Luzon Island: Bataan Prov.: 0.1 km N Mt. Natib peak, 1150 m (FMNH 183389, 183391, 183392, 183414–183416, 183418, 183421–183424); 0.3 km N, 0.1 km W Mt. Natib peak, 1000 m (FMNH 183382–183386, 183388, 183390, 183405–183413, 183417, 183419, 183425); 0.7 km N, 0.2 km W Mt. Natib peak, 900 m (FMNH 183341–183381, 183387, 183393–183404).

Zambales Prov.: Palauig Munic.: Brgy. Salasa, Mt. Tapulao, 860 m (FMNH 178310, 178326–178330); Palauig Munic.: Brgy. Salasa, Mt. Tapulao, 925 m (FMNH 183529–183545); Palauig Munic.: Brgy. Salasa, Mt. Tapulao, 1200 m (FMNH 178276–178292, 178331–178333, 178338–178343, 179434–179442); Palauig Munic.: Brgy. Salasa, Mt. Tapulao, 1690 m (FMNH 178293–178309, 178311–178325, 178334–178337, 178344–178357).

ETYMOLOGY—An adjective from the name of the province, Zambales, from which the majority of the specimens originated, and the name of the geological region (the Zambales Range) that includes the type locality.

DIAGNOSIS AND DESCRIPTION—*Apomys zambalensis* is the second largest known species of *Megapomys,* with a total length averaging 278–289 mm and weight averaging 84–94 g

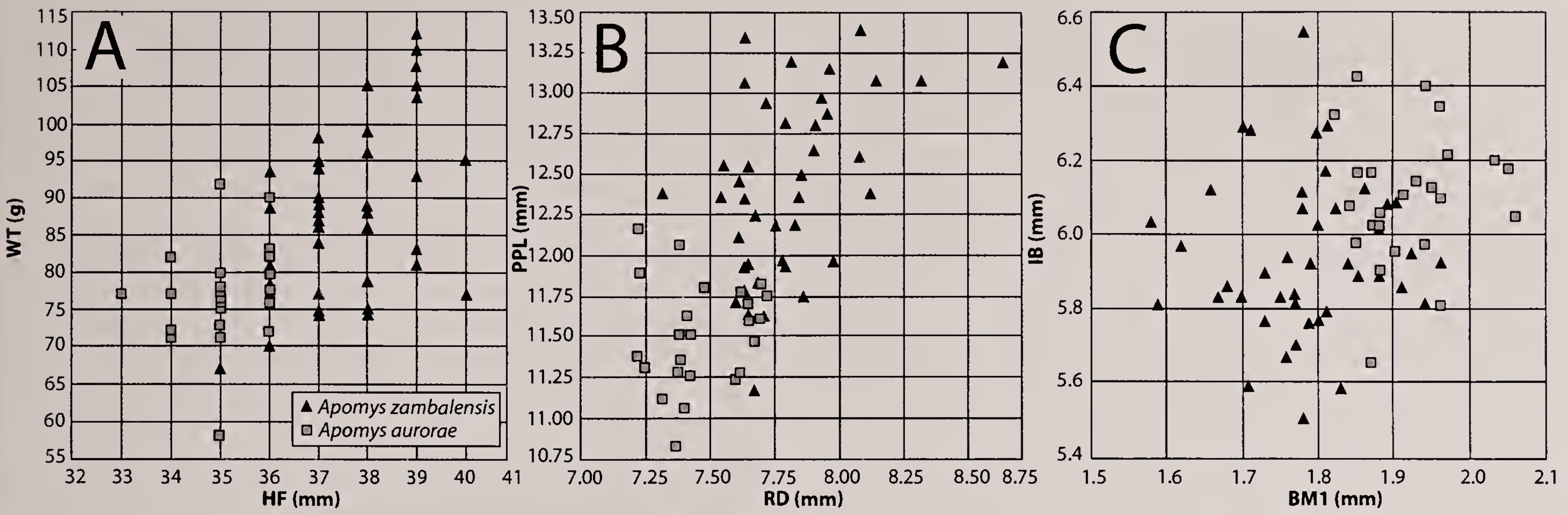


FIG. 45. Bivariate plots of measurements comparing *Apomys aurorae* and *A. zambalensis* spp. nov. (**A**) Length of hind foot (HF) and weight (WT). (**B**) Rostral depth (RD) and postpalatal length (PPL). (**C**) Breadth of M^1 (BM^1) and interorbital breadth (IB).

(Table 15). The tail is typically 94–100% of the length of the head and body, making it one of the longest-tailed species in the subgenus. The dorsal fur is shorter and paler than that of most species, with a bright rusty-orange appearance (Fig. 2A). The ventral fur is pale to medium gray at the base, and white with an ochraceous wash at the tips that varies between individuals from slight to heavy. The ears are large, usually 22–23 mm, and less heavily pigmented than those of most other *Megapomys*. The tail is sharply bicolored, heavily pigmented dorsally but nearly white ventrally. The rusty-brown dorsal color extends onto the forelimb in a dark stripe that is bounded by pale orange, barely reaching to the base of the foot. The hind foot is long (usually 36–39 mm) and broad, with digit 5 reaching nearly to the middle joint of digit 4. It is nearly white dorsally, sometimes with a few dark hairs. The ventral side of the hind foot is lightly pigmented, with some pigment on interdigital pad 4 and the hypothenar. The hallux is long, reaching about to the top of the adjacent interdigital pad (Fig. 10I).

The skull of *A. zambalensis* (Fig. 46) is large, with basioccipital length averaging 34–38 mm (Table 15); only that of *A. magnus* is larger overall. The rostrum is long and robust,

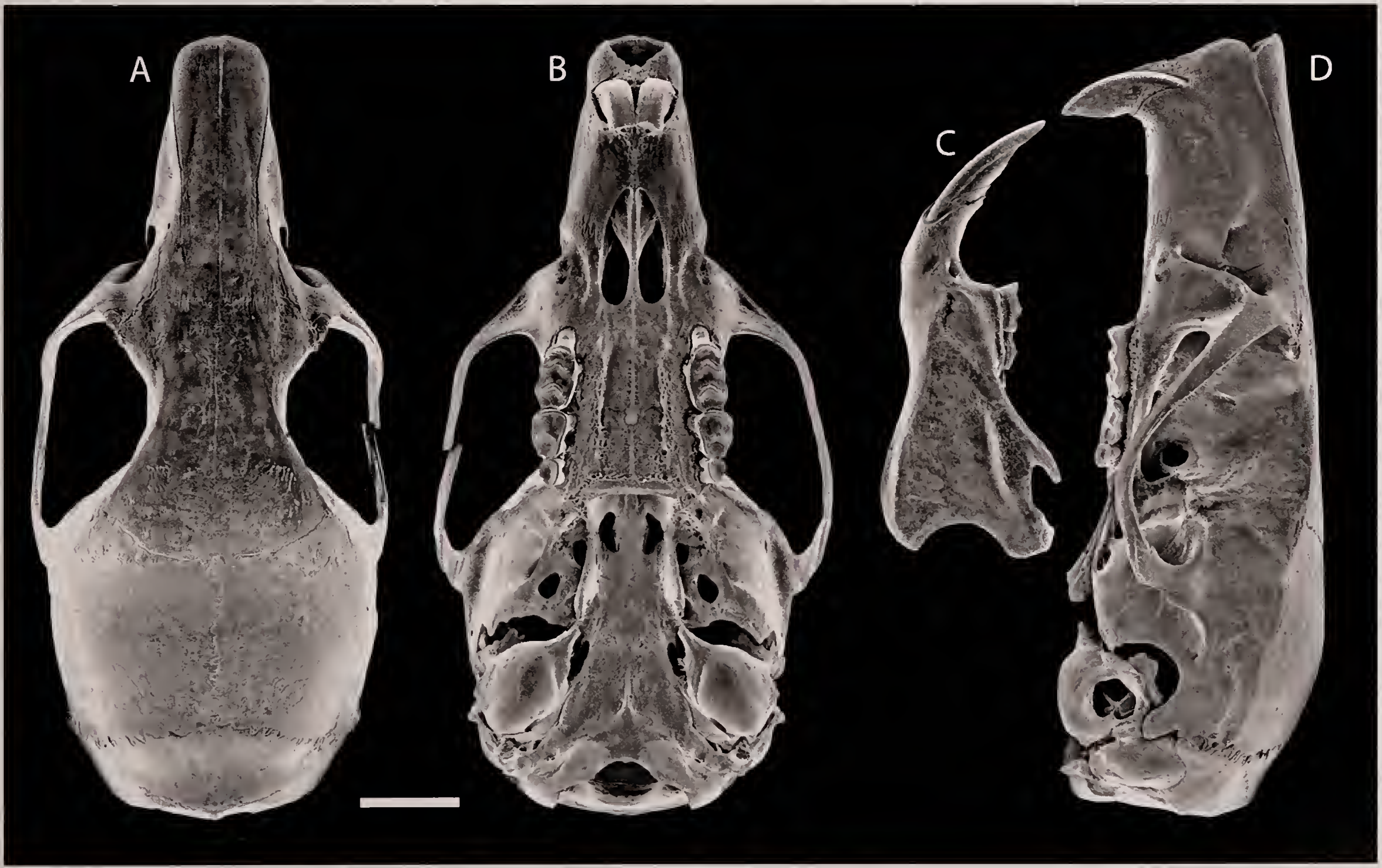


FIG. 46. Dorsal (**A**), ventral (**B**), and lateral (**D**) views of the cranium and lateral view of the mandible (**C**) of *Apomys zambalensis* sp. nov. (FMNH 183420, holotype); scale bar = 5 mm.

and the braincase is sturdy and somewhat elongate and flattened. The incisive foramina are unusually broad, especially in the posterior portions. The bony palate is of typical width and is moderately heavily pitted over its posterior portion. The maxillary toothrows are of roughly average length and width and diverge slightly posteriorly. The postpalatal region is elongated. The foramen in the bulla for the stapedial artery is relatively large and conspicuous (the "datae pattern"; Fig. 5B). The interparietal is variable in shape but usually is wide anteroposteriorly. The mandible (Fig. 46C) is average in depth, with a shorter than average coronoid process, average angular process, and rather deep concavity between the condylar and angular processes.

As noted above, the analysis of mitochondrial DNA shows only slight divergence between our two samples from Mt. Tapulao and Mt. Natib (Fig. 7). A PCA of craniodental measurements, discussed above (Fig. 23; Table 7) that included the closely related *A. aurorae* and *A. magnus*, as well as the holotype of the geographically adjacent *A. sacobianus*, showed virtually complete overlap of individuals from these two mountains on both the first component, which primarily indicated size, and the second component, which loaded heavily (and positively) on diastema length and postpalatal length and (negatively) on interorbital breadth, palatal breadth at M^1, and width of the zygomatic plate. Additionally, we are unable to detect any discrete cranial features to separate these samples. On the basis of these genetic and morphological data, we consider these populations to represent a single species, and we predict that individuals from geographically intermediate populations will bridge the current slight genetic gap between northern and southern populations.

The karyotype of *A. zambalensis* on the basis of eight males and seven females from Mt. Natib, Bataan Province (FMNH 183361, 183362, 183364, 183367, 183368, 183370–183373, 183376–183379, 183387, 183391), has $2n = 44$, $FN \geq 58$ (Fig. 8C). The autosomal complement consists of two pairs of large submetacentric, two pairs of medium-sized subtelocentric, two pairs of very small metacentric or submetacentric, and 15 pairs of small to large-sized telocentric or subtelocentric elements. The X chromosome is medium-sized and submetacentric, and the Y chromosome is small and telocentric.

COMPARISONS—*Apomys zambalensis* is easily distinguished externally from other *Megapomys* by its large size, comparatively pale, bright rusty-brown fur, and pale ears and ventral surface of the hind feet. Similarly, the skull is easily distinguished by its large size, exceeding all species except *A. magnus*. *Apomys zambalensis* is easily distinguished from its closest relative, *A. aurorae*, as described above; *A. aurorae* is smaller, with darker brown dorsal fur, dark hairs on the dorsal side of the hind foot and more heavily pigmented soles, a short hallux, a longer and more robust rostrum and braincase (Fig. 45), and a larger stapedial foramen in the bulla. As reflected in the PCA (Fig. 23; Table 7) of *A. zambalensis*, *A. aurorae*, *A. magnus*, and *A. sacobianus*, *A. zambalensis* typically differs from *A. aurorae* in having a narrower M^1 and low braincase, but longer diastema, incisive foramina, and postpalatal region (Fig. 45). The hallux of *A. zambalensis* is long, whereas that of *A. aurorae* is short (Fig. 10G). Both *A. zambalensis* and *A. aurorae* possess the "datae pattern" of basicranial circulation (Fig. 5B), but *A. aurorae* has a smaller stapedial foramen than *A. zambalensis*.

Apomys zambalensis differs from *A. magnus*, also closely related, as described above under that species; *A. magnus* is slightly larger and generally darker, with dark ears and dark soles on the hind feet, with a broader M^1, longer maxillary toothrow, and broader palate (Fig. 43). These differences are clearly apparent in a PCA of craniodental measurements (Fig. 23; Table 7).

As described above, *A. sierrae* is somewhat smaller than *A. zambalensis* in external features and is much darker dorsally and ventrally, with much dark hair on the dorsal surface of the hind foot and dark pigment on the ventral surface, and it has a short hallux. *Apomys sierrae* has the "abrae pattern" of basicranial carotid circulation (Fig. 5A) and is smaller in breadth of M^1, postpalatal length, and diastema length (Fig. 40). The PCA of craniodental measurements described above (Fig. 38; Table 14) shows no difference in size (PC1); there is overlap, but with substantially different averages along PC2, which loads heavily on the dental features, diastema length, and postpalatal length that are individually apparent as differences. Given these morphological differences and the clear evidence of genetic monophyly and intervening species in the phylogeny, we conclude that they represent distinct species.

DISTRIBUTION—We have documented *A. zambalensis* along our elevational transects on Mt. Tapulao from 860 to 1690 m and on Mt. Natib from 900 to 1150 m (Figs. 15, 35; Balete et al., 2009). We had no sampling areas below these elevations on either transect, so we do not know the lower limit of the species' distribution with certainty; because it was common at our lowest sites, we suspect that it also occurs somewhat lower. The upper boundary is also uncertain, because we have no data between 1690 and 2024 m, but we suspect that it lies near 1800 m, the elevation at which primary mossy forest begins (Balete et al., 2009). We lack data from other mountains in this region, but the presence of *A. zambalensis* on Mts. Tapulao and Natib (Figs. 3, 35) leads us to suspect that it occurs throughout the Zambales Mountains and on Mt. Mariveles on the Bataan Peninsula at elevations above about 700 m. If this is so, it makes *A. zambalensis* one of the more widely distributed species of *Megapomys*.

Discussion

The Status of Discovery of Philippine Mammalian Diversity

The discovery and description of seven previously unknown species of mammals may surprise some people, especially since all but one come from within 150 km of Manila (Fig. 3), a metropolitan area with roughly 15 million people, and especially in the current millennium, when it is widely assumed that, although some less conspicuous organisms are poorly known, mammals have generally been well documented. Our studies in the field and museum show that this widespread assumption is not well-founded. With one species of *Archboldomys* (Balete et al., 2006), two species of *Rhynchomys* (Balete et al., 2007), and a new genus and species of mouse (*Musseromys gulantang*; Heaney et al., 2009) already described from the same areas on Luzon, as well as our ongoing studies indicating that many additional new species in other genera were obtained in the same surveys, it is clear that a great deal of the mammalian diversity on Luzon, and perhaps in the Philippines as a whole, has been unknown to the scientific and conservation communities in the past, and it is likely that many species remain unknown.

One might ask how long this poor state of knowledge will persist in the future. Our studies of Luzon mammals have been conducted in the context of predictive biogeographic models and thus have been focused on those places most likely to result in the discovery of new biological diversity. We predict that locally endemic mammals will be found on individual mountains or on mountain ranges that reach above 1000 m elevation and are isolated from other such mountainous areas by elevations below 300 m that are at least 10 km wide (Heaney & Rickart, 1990; Heaney et al., 2000; Heaney, 2001, 2004; Rickart et al., 2010). Although our field surveys are not yet complete, we predict that within a few more years, few scientifically unknown mammals will remain on Luzon, with one exception. Because our models are discrete and predictive, they can be (and are being) tested, and so our prediction of a declining curve of discovery will soon be either validated or falsified. Thus, on the basis of current and planned surveys, we will soon know whether mammalian diversity on Luzon is well documented or whether our models were incorrect, and therefore an unknown, but potentially great, number of species remains to be found.

The one exception noted above refers to insectivorous bats. This group is notoriously difficult to capture using our standard sampling procedure, the use of mist nets, and we know that some "species" are actually groups of cryptic species (e.g., Ingle & Heaney, 1992; Sedlock & Weyandt, 2009). We explicitly acknowledge that we have not documented this group adequately and look forward to the results of the increased use of alternative methods (such as bat traps, V-nets, and tunnel traps; e.g., Alviola, 2008; Sedlock et al., 2008, this volume; Alviola et al., this volume; Balete et al., this volume) and evaluations using molecular genetics.

This discussion has referred only to the mammals of Luzon Island. The predictive biogeographic models that we have developed (Heaney & Rickart, 1990; Heaney, 2000, 2001, 2004; Rickart et al., 2011) refer to geographic features (e.g., elevational patterns of distribution, elevation of mountains, degree of isolation of mountains, etc.) that are relevant to other still very incompletely surveyed areas in the Philippines. Our discovery of a previously unknown species of *Batomys* from southeastern Mindanao (Balete et al., 2008) is consistent with the patterns we have noted on Luzon, and it implies that many subcenters of mammalian endemism, and therefore many currently unknown species of mammals, remain to be documented on Mindanao. The recent description of *Crocidura panayensis* from Panay Island (Hutterer, 2007) implies to us that similar conditions exist on the islands that formed large aggregate islands during Pleistocene periods of low sea level and suggests that similarly intensive surveys of mammalian diversity on those islands are warranted.

Geographic Distribution Patterns in *Megapomys*

The distribution of species in the subgenus *Megapomys* is distinctly nonrandom, with six patterns that can be readily identified at this time.

1) Species of *Megapomys* extend from northernmost Luzon to Mt. Banahaw, but no further south on Luzon (Fig. 3). Intensive surveys of small mammals on the Bicol Peninsula of southern Luzon, on Mt. Labo, Saddle Peak, Mt. Isarog, Mt. Malinao, and Mt. Bulusan, using the same techniques that easily capture them in central and northern Luzon, have failed to capture any *Megapomys*, although the smaller species of *Apomys* are often present and common (Rickart et al., 1991; Balete & Heaney, 1997; Heaney et al., 1999; L. R. Heaney, unpubl. data and specimens, FMNH). The elevation of the highest point connecting the Bicol Peninsula and central Luzon is only about 4 m above sea level, and this area of low elevation is extensive, thus significantly isolating the mountains of southern Luzon from those of central and northern Luzon.
2) All of the species of *Megapomys* occur on Luzon only at elevations above 450 m, with few records below 800 m (Fig. 15), even in areas of dense sampling effort where forest is present (e.g., the Sierra Madre; Duya et al., 2007). The one possible exception is *A. sacobianus*, known from a single specimen taken near the Sacobia River "just above the point where it emerges from the foothills of the Zambales Mountains onto the plains of Pampanga" (Johnson, 1962). From maps of the area, we estimate this to be 300 m. Each of the mountain masses has one or more species of *Megapomys* from this lower point up to the highest peak of the mountain. These data suggest that the large areas of Luzon below 450 m do not, and did not before deforestation, support populations of *Megapomys* (except perhaps rarely between 450 and 300 m). On the other hand, every mountain mass with a peak above about 1000 m that has been intensively surveyed has at least one species present. Clearly, the species of *Megapomys* are principally animals of montane and mossy forest. We note, however, that *A. sierrae* has been documented on Palaui Island, a small island off the NE tip of Luzon, at ca. 150 m. Specimens of *A. sierrae* have been taken only above about 750 m in the adjacent areas of Cagayan Province on Luzon Island. We suspect the lower elevational range is associated with the fact that Palaui is a small island with reduced species richness, as seen among small mammals on Dinagat and Siargao islands, which lie off the NE coast of Mindanao (Heaney and Rabor, 1982: Heaney et al., 1998); further study is needed.
3) Each species of *Megapomys* is associated with a single mountain range or individual mountain that is isolated from other such mountains by lowland areas at 300 m or lower. Each such mountainous area is thus an island of montane or mossy forest habitat in a "sea" of lowland forest (or, in recent centuries, agricultural lands). In cases in which the mountain range is very extensive, as with the Central Cordillera and the Sierra Madre, the species are similarly widespread (i.e., *A. abrae*, *A. datae*, and *A. sierrae*). In cases in which the mountain range is somewhat smaller, such as the Zambales Mountains (which in this case we define to include the mountains of the Bataan Peninsula), the range is smaller (i.e., *A. zambalensis*). In cases in which the mountain range is very small, the range of the species is very small (e.g., *A. minganensis* and *A. aurorae* in the Mingan Mountains and *A. banahao* and *A. magnus* on Mt. Banahaw). The only exception to this pattern currently evident is the occurrence of *A. zambalensis* on Mt. Natib (on the Bataan Peninsula) and on the Zambales Mountains, which are separated from one another by a lowland area that drops to about 200 m. However, the distance along the highest ridge connecting Mt. Natib to Zambales that is below 450 m is less than

10 km wide and is made up of fairly steep, rugged slopes, not flat lowlands. This might provide some clue as to the precise conditions that prevent the movement of *Megapomys* from one mountain mass to another.

4) Two species of *Megapomys* occur on mountains over most of central and northern Luzon, although which species are present varies between mountain masses (Fig. 15). In the Central Cordillera, *A. abrae* occurs from about 900 to 2200 m, and *A. datae* from about 1500 m to higher than 2800 m. The former occurs most often in relatively open (often disturbed) and drier habitats, and the latter in more mature, moister forest (Rickart et al., 2011). On Mt. Banahaw, *A. magnus* occurs from about 800 to 1465 m, and *A. banahao* from 1465 m up to at least 1800 m. In the Mingan Mountains, *A. aurorae* occurs from about 750 to ca. 1550 m, and *A. minganensis* from 1550 to 1750 m. In the Zambales Mountains, *A. zambalensis* occurs from about 850 to about 1750 m, and *A. brownorum* near the peak at about 2050 m. These data show that over most of central and northern Luzon, two species of *Megapomys* usually occur on any given mountain mass, with one species occurring from the lower limits of montane forest elements (which begin to appear at about 500 m, but often are sparse and widely scattered below 800 m) up to the beginnings of prime mossy forest at about 1500 m, and the other species occurring in mossy forest from about 1500 m up to the peak. Current data are limited, but they suggest that the species at the lower elevation will often occur in more open and drier habitat at the upper edge of their ranges and that syntopy between individuals of the two species will be present but not extensive.
5) Species that occur within the same mountain mass are not sister-species and most often are rather distantly related (Fig. 7). For example, on Mt. Banahaw (*A. banahao* and *A. magnus*) and the Zambales Mountains (*A. brownorum* and *A. zambalensis*), the co-occurring pairs are distantly related to one another. In the Mingan Mountains, *A. aurorae* and *A. minganensis* are more closely related, but they are still separated by considerable genetic distance and several nodes in the phylogenetic tree. Only in the Central Cordillera is this pattern not directly supported: *A. abrae* and *A. datae* appear to be sister-taxa on the basis of Figure 5, but we question the accuracy of the mitochondrial data in this case because our preliminary nuclear sequence data indicate that they are more distantly related (S. J. Steppan, unpubl. data). Instead of close relatives occupying nearby localities in the same mountain region, they occupy similar elevations in different mountains.
6) There appears to be considerable ecological conservatism, with all but one (*A. abrae*) of the species in clades B and C (Fig. 7) occurring in high-elevation mossy forest and all but one (*A. minganensis*) of the species in clade D occurring in montane forest, primarily below 1500 m. This pattern suggests diversification among *Megapomys* within particular portions of the elevational gradient throughout northern and central Luzon.

Taken together, these six patterns imply a long history of diversification within the subgenus *Megapomys*, with diversification processes that usually involved ecological (habitat and climate) and geographic (topographic and geological) components. Furthermore, our ongoing studies of other endemic Philippine murid genera on Luzon (*Archboldomys*, *Batomys*, *Chrotomys*, *Musseromys*, and *Rhynchomys*) suggest that these genera also have undergone extensive diversification. These patterns and processes will be considered in detail elsewhere following the necessary taxonomic studies.

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Appendix I

Location and GenBank accession numbers for sequenced individuals. Brgy., Barangay; Munic., Municipality; Prov., Province.

Genus	Species	Voucher	Island/Province	Locality	GenBank accession
Apomys	*abrae*	FMNH 169051	Luzon/Kalinga Prov.	Balbalan Munic.	HM371053
Apomys	*abrae*	FMNH 170904	Luzon/Kalinga Prov.	Balbalan Munic.	HM371054
Apomys	*abrae*	FMNH 170915	Luzon/Kalinga Prov.	Balbalan Munic., Balbalasang Brgy.: Mapga	HM371055
Apomys	*abrae*	FMNH 170929	Luzon I/Kalinga Prov.	Balbalan Munic., Balbalasang Brgy.: Mapga	HM371056
Apomys	*abrae*	FMNH 188293	Luzon/Mountain Prov.	Mt. Data: 1.0 km N, 1.25 km E south peak	HM371057
Apomys	*abrae*	FMNH 188294	Luzon/Mountain Prov.	Mt. Data: 0.9 km N, 1.75 km E south peak	HM371059
Apomys	*abrae*	FMNH 188297	Luzon/Mountain Prov.	Mt. Data: 0.9 km N, 1.75 km E south peak	HM371058
Apomys	*abrae*	FMNH 193867	Luzon/Mountain Prov.	0.4 km N Barlig Munic. Hall	HM371060
Apomys	*abrae*	FMNH 193872	Luzon/Mountain Prov.	0.6 km N Barlig Munic. Hall	HM371061
Apomys	*abrae*	FMNH 193876	Luzon/Mountain Prov.	0.6 km N Barlig Munic. Hall	HM371062
Apomys	*abrae*	FMNH 62724	Luzon/Mountain Prov.	Mt. Data	HM371049
Apomys	*abrae*	FMNH 62749	Luzon/Abra Prov.	Massisiat	HM371050
Apomys	*abrae*	FMNH 92759	Luzon/Ilocos Norte Prov.	Mt. Simminublar (Mt. Sicapoo)	HM371051
Apomys	*abrae*	FMNH 92760	Luzon/Ilocos Norte Prov.	Mt. Simminublar (Mt. Sicapoo)	HM371052
Apomys	*aurorae*	FMNH 190919	Luzon/Aurora Prov.	Dingalan Munic.: 2.1 km S, 2.9 km W Mingan peak	HM371035
Apomys	*aurorae*	FMNH 190921	Luzon/Aurora Prov.	Dingalan Munic.: 2.1 km S, 2.9 km W Mingan peak	HM371036
Apomys	*aurorae*	FMNH 190928	Luzon/Aurora Prov.	Dingalan Munic.: 2.1 km S, 2.9 km W Mingan peak	HM371037
Apomys	*aurorae*	FMNH 190932	Luzon/Aurora Prov.	Dingalan Munic.: 2.1 km S, 2.9 km W Mingan peak	HM371038
Apomys	*banahao*	FMNH 179453	Luzon/Quezon Prov.	Mt. Banahaw, Brgy. Lalo	HM371078
Apomys	*banahao*	FMNH 179456	Luzon/Quezon Prov.	Mt. Banahaw, Brgy. Lalo	HM371079
Apomys	*banahao*	FMNH 179459	Luzon/Quezon Prov.	Mt. Banahaw, Brgy. Lalo	HM371080
Apomys	*banahao*	FMNH 179462	Luzon/Quezon Prov.	Mt. Banahaw, Brgy. Lalo	HM371081
Apomys	*banahao*	FMNH 179465	Luzon/Quezon Prov.	Mt. Banahaw, Brgy. Lalo	HM371082
Apomys	*banahao*	FMNH 179505	Luzon/Quezon Prov.	Mt. Banahaw, Brgy. Lalo	HM371083
Apomys	*banahao*	FMNH 179511	Luzon/Quezon Prov.	Mt. Banahaw, Brgy. Lalo	HM371084
Apomys	*banahao*	FMNH 179515	Luzon/Quezon Prov.	Mt. Banahaw, Brgy. Lalo	HM371085
Apomys	*brownorum*	FMNH 183495	Luzon/Zambales Prov.	Palauig Munic.: Brgy. Salasa: Mt. Tapulao	HM371086
Apomys	*brownorum*	FMNH 183497	Luzon/Zambales Prov.	Palauig Munic.: Brgy. Salasa: Mt. Tapulao	HM371087
Apomys	*brownorum*	FMNH 183499	Luzon/Zambales Prov.	Palauig Munic.: Brgy. Salasa: Mt. Tapulao	HM371088
Apomys	*brownorum*	FMNH 183501	Luzon/Zambales Prov.	Palauig Munic.: Brgy. Salasa: Mt. Tapulao	HM371089
Apomys	*brownorum*	FMNH 183503	Luzon/Zambales Prov.	Palauig Munic.: Brgy. Salasa: Mt. Tapulao	HM371090
Apomys	*camiguinensis*	FMNH 154816	Camiguin	Mt. Timpoong, 2 km N, 6.5 km W Mahinog	AY324476
Apomys	*camiguinensis*	FMNH 154854	Camiguin	Mt. Timpoong, 2 km N, 6.5 km W Mahinog	AY324477
Apomys	*datae*	FMNH 167243	Luzon/Kalinga Prov.	Balbalan Munic., Balbalasang: Magdalao	AY324463
Apomys	*datae*	FMNH 167358	Luzon/Kalinga Prov.	Balbalan Munic., Balbalasang: Magdalao	AY324464
Apomys	*datae*	FMNH 169098	Luzon/Kalinga Prov.	Balbalan Munic., Balbalasang Brgy.: Am-licao	HM371064
Apomys	*datae*	FMNH 169103	Luzon/Kalinga Prov.	Balbalan Munic., Balbalasang Brgy.: Am-licao	HM371065
Apomys	*datae*	FMNH 169108	Luzon/Kalinga Prov.	Balbalan Munic., Balbalasang Brgy.: Am-licao	HM371066
Apomys	*datae*	FMNH 169110	Luzon/Kalinga Prov.	Balbalan Munic., Balbalasang Brgy.: Am-licao	HM371067
Apomys	*datae*	FMNH 169120	Luzon/Kalinga Prov.	Balbalan Munic., Balbalasang Brgy.: Am-licao	HM371068

Appendix I

Continued.

Genus	Species	Voucher	Island/Province	Locality	GenBank accession
Apomys	*datae*	FMNH 175682	Luzon/Kalinga Prov.	Balbalan Munic., Balbalasang Brgy.: Mt. Bali-it	HM371069
Apomys	*datae*	FMNH 175683	Luzon/Kalinga Prov.	Balbalan Munic., Balbalasang Brgy.: Mt. Bali-it	HM371070
Apomys	*datae*	FMNH 175708	Luzon/Kalinga Prov.	Balbalan Munic., Balbalasang Brgy.: Mt. Bali-it	HM371071
Apomys	*datae*	FMNH 188298	Luzon/Mountain Prov.	Mt. Data: 0.1 km E south peak	HM371072
Apomys	*datae*	FMNH 188300	Luzon/Mountain Prov.	Mt. Data: 0.1 km E south peak	HM371073
Apomys	*datae*	FMNH 188305	Luzon/Mountain Prov.	Mt. Data: 0.1 km E south peak	HM371074
Apomys	*datae*	FMNH 193554	Luzon/Mountain Prov.	0.5 km N, 0.5 W Mt. Amuyao peak	HM371075
Apomys	*datae*	FMNH 193655	Luzon/Mountain Prov.	1.0 km N, 1.0 km W Mt. Amuyao peak	HM371076
Apomys	*datae*	FMNH 193877	Luzon/Mountain Prov.	0.6 km N Barlig Munic. Hall	HM371077
Apomys	*datae*	FMNH 62709	Luzon/Mountain Prov.	Mt. Data	HM371063
Apomys	*gracilirostris*	CMNH 646	Mindoro/Mindoro Oriental Prov.	North ridge approach to Mt. Halcon, Hanglo	AY324465
Apomys	*gracilirostris*	CMNH 648	Mindoro/Mindoro Oriental Prov.	North ridge approach to Mt. Halcon, Hanglo	AY324466
Apomys	*hylocoetes*	FMNH 147871	Mindanao/Bukidnon Prov.	Mt. Katanglad range, 16.5 km S, 4 km E Camp Phillips	AY324467
Apomys	*hylocoetes*	FMNH 147914	Mindanao/Bukidnon Prov.	Mt. Katanglad range, 16.5 km S, 4 km E Camp Phillips	AY324468
Apomys	*hylocoetes*	FMNH 148149	Mindanao/Bukidnon Prov.	Mt. Katanglad range, 16.5 km S, 4 km E Camp Phillips	AY324469
Apomys	*insignis*	FMNH 147911	Mindanao/Bukidnon Prov.	Mt. Katanglad range, 16.5 km S, 4 km E Camp Phillips	AY324470
Apomys	*insignis*	FMNH 147915	Mindanao/Bukidnon Prov.	Mt. Katanglad range, 16.5 km S, 4 km E Camp Phillips	AY324471
Apomys	*insignis*	FMNH 147924	Mindanao/Bukidnon Prov.	Mt. Katanglad range, 16.5 km S, 4 km E Camp Phillips	AY324473
Apomys	*insignis*	FMNH 148160	Mindanao/Bukidnon Prov.	Mt. Katanglad range, 16.5 km S, 4 km E Camp Phillips	AY324472
Apomys	*magnus*	FMNH 178395	Luzon/Quezon Prov.	Mt. Banahaw, Brgy. Lalo	HM371039
Apomys	*magnus*	FMNH 178396	Luzon/Quezon Prov.	Mt. Banahaw, Brgy. Lalo	HM371040
Apomys	*magnus*	FMNH 183569	Luzon/Quezon Prov.	Tayabas Munic.: Brgy. Lalo: Mt. Banahaw, Idoro	HM371041
Apomys	*magnus*	FMNH 183570	Luzon/Quezon Prov.	Tayabas Munic.: Brgy. Lalo: Mt. Banahaw, Idoro	HM371042
Apomys	*magnus*	FMNH 183573	Luzon/Quezon Prov.	Tayabas Munic.: Brgy. Lalo: Mt. Banahaw, Hasa-an	HM371043
Apomys	*magnus*	FMNH 183574	Luzon/Quezon Prov.	Tayabas Munic.: Brgy. Lalo: Mt. Banahaw, Hasa-an	HM371044
Apomys	*microdon*	FMNH 167241	Luzon/Kalinga Prov.	Balbalan Munic., Balbalasang: Magdalao	AY324478
Apomys	*microdon*	FMNH 167242	Luzon/Kalinga Prov.	Balbalan Munic., Balbalasang: Magdalao	AY324479
Apomys	*microdon*	USNM 458907	Luzon/Camarines Sur Prov.	Mt. Isarog	AY324480
Apomys	*microdon*	USNM 458919	Luzon/Camarines Sur Prov.	Mt. Isarog	AY324481
Apomys	*minganensis*	FMNH 190778	Luzon/Aurora Prov.	Dingalan Munic.: 0.9 km S, 0.3 km W Mingan peak	HM371045
Apomys	*minganensis*	FMNH 190781	Luzon/Aurora Prov.	Dingalan Munic.: 0.9 km S, 0.3 km W Mingan peak	HM371046
Apomys	*minganensis*	FMNH 190782	Luzon/Aurora Prov.	Dingalan Munic.: 0.9 km S, 0.3 km W Mingan peak	HM371047
Apomys	*minganensis*	FMNH 190861	Luzon/Aurora Prov.	Dingalan Munic.: 0.9 km S, 0.3 km W Mingan peak	HM371048
Apomys	*musculus*	USNM 458925	Luzon/Camarines Sur Prov.	Mt. Isarog	AY324482
Apomys	*musculus*	USNM 458913	Luzon/Camarines Sur Prov.	Mt. Isarog	AY324483
Apomys	*sierrae*	FMNH 176562	Luzon/Cagayan Prov.	Gonzaga Munic., Brgy. Magrafil, Mt. Cagua, Sitio Masok	HM370984
Apomys	*sierrae*	FMNH 176564	Luzon/Cagayan Prov.	Gonzaga Munic., Brgy. Magrafil, Mt. Cagua, Sitio Masok	HM370985
Apomys	*sierrae*	FMNH 176566	Luzon/Cagayan Prov.	Gonzaga Munic., Brgy. Magrafil, Mt. Cagua, Sitio Masok	HM370986
Apomys	*sierrae*	FMNH 176568	Luzon/Cagayan Prov.	Gonzaga Munic., Brgy. Magrafil, Mt. Cagua, Sitio Masok	HM370987
Apomys	*sierrae*	FMNH 176570	Luzon/Cagayan Prov.	Gonzaga Munic., Brgy. Magrafil, Mt. Cagua, Sitio Masok	HM370988

Appendix I

Continued.

Genus	Species	Voucher	Island/Province	Locality	GenBank accession
Apomys	*sierrae*	FMNH 180302	Luzon/Cagayan Prov.	Penablanca Munic., Brgy. Lapi, Sitio Baua, Mt. Cetaceo	HM370989
Apomys	*sierrae*	FMNH 180310	Luzon/Cagayan Prov.	Penablanca Munic., Brgy. Lapi, Sitio Baua, Mt. Cetaceo	HM370990
Apomys	*sierrae*	FMNH 180320	Luzon/Cagayan Prov.	Penablanca Munic., Brgy. Lapi, Sitio Baua, Mt. Cetaceo	HM370991
Apomys	*sierrae*	FMNH 180330	Luzon/Cagayan Prov.	Penablanca Munic., Brgy. Lapi, Sitio Baua, Mt. Cetaceo	HM370992
Apomys	*sierrae*	FMNH 180340	Luzon/Cagayan Prov.	Penablanca Munic., Brgy. Lapi, Sitio Baua, Mt. Cetaceo	HM370993
Apomys	*sierrae*	FMNH 180365	Luzon/Quirino Prov.	Nagtipunan Munic., Brgy. Matmad, Sitio Mangitagud, Mungiao Mtns	HM370994
Apomys	*sierrae*	FMNH 180367	Luzon/Quirino Prov.	Nagtipunan Munic., Brgy. Matmad, Sitio Mangitagud, Mungiao Mtns	HM370995
Apomys	*sierrae*	FMNH 180369	Luzon/Quirino Prov.	Nagtipunan Munic., Brgy. Matmad, Sitio Mangitagud, Mungiao Mtns	HM370996
Apomys	*sierrae*	FMNH 180371	Luzon/Quirino Prov.	Nagtipunan Munic., Brgy. Matmad, Sitio Mangitagud, Mungiao Mtns	HM370997
Apomys	*sierrae*	FMNH 180373	Luzon/Quirino Prov.	Nagtipunan Munic., Brgy. Matmad, Sitio Mangitagud, Mungiao Mtns	HM370998
Apomys	*sierrae*	FMNH 185806	Luzon/Cagayan Prov.	3.5 km SW Mt. Cetaceo peak	HM370999
Apomys	*sierrae*	FMNH 185816	Luzon/Cagayan Prov.	2.0 km SW Mt. Cetaceo peak	HM371000
Apomys	*sierrae*	FMNH 185871	Luzon/Cagayan Prov.	1.5 km SW Mt. Cetaceo peak	HM371001
Apomys	*sierrae*	FMNH 185906	Luzon/Cagayan Prov.	3.5 km SW Mt. Cetaceo peak	HM371002
Apomys	*sierrae*	FMNH 185943	Luzon/Cagayan Prov.	2.0 km SW Mt. Cetaceo peak	HM371003
Apomys	*sierrae*	FMNH 185948	Luzon/Cagayan Prov.	3.5 km SW Mt. Cetaceo peak	HM371004
Apomys	*sierrae*	FMNH 186728	Luzon/Nueva Vizcaya Prov.	Quezon Munic., 1.3 km NE Mt. Palali	HM371005
Apomys	*sierrae*	FMNH 186730	Luzon/Nueva Vizcaya Prov.	Quezon Munic., 1.3 km NE Mt. Palali	HM371006
Apomys	*sierrae*	FMNH 186736	Luzon/Nueva Vizcaya Prov.	Quezon Munic., 1.3 km NE Mt. Palali	HM371007
Apomys	*sierrae*	FMNH 186739	Luzon/Nueva Vizcaya Prov.	Quezon Munic., 1.3 km NE Mt. Palali	HM371008
Apomys	*sierrae*	FMNH 186763	Luzon/Nueva Vizcaya Prov.	Quezon Munic., Mt. Palali Peak	HM371009
Apomys	*sierrae*	FMNH 186765	Luzon/Nueva Vizcaya Prov.	Quezon Munic., Mt. Palali Peak	HM371010
Apomys	*sierrae*	FMNH 191232	Palaui/Cagayan Prov.	Sta. Ana Munic., Brgy. San Vicente, 4.25 km S of Cape Engano Lighthouse	HM371011
Apomys	"sp. A/C"	USNM 458747	Negros/Negros Oriental Prov.	3 km N, 17 km W Dumaguete, Mt. Guinsayawan	AY324486
Apomys	"sp. A/C"	USNM 458751	Negros/Negros Oriental Prov.	3 km N, 17 km W Dumaguete, Mt. Guinsayawan	AY324487
Apomys	"sp. A/C"	FMNH 135715	Sibuyan/Romblon Prov.	Magdiwang, 4.5 km S, 4 km E; NW slope Mt. Guitinguitin	AY324484
Apomys	"sp. A/C"	FMNH 137024	Sibuyan/Romblon Prov.	Magdiwang, 4.5 km S, 4 km E; NW slope Mt. Guitinguitin	AY324485
Apomys	"sp. B"	FMNH 145698	Sibuyan/Romblon Prov.	Magdiwang, 6.75 km S, 4.5 km E; NW slope Mt. Guitinguitin	AY324488
Apomys	"sp. B"	FMNH 145699	Sibuyan/Romblon Prov.	Magdiwang, 4.5 km S, 4 km E; NW slope Mt. Guitinguitin	AY324489
Apomys	"sp. F"	USNM 458762	Leyte/Leyte Prov.	10 km N, 4.5 km E Baybay	AY324474
Apomys	"sp. F"	USNM 459844	Biliran/Leyte Prov.	5 km N, 10 km E Naval	AY324475
Apomys	*zambalensis*	FMNH 178276	Luzon/Zambales Prov.	Mt. High Peak, Palauig Munic., Brgy. Salasa	HM371012
Apomys	*zambalensis*	FMNH 178282	Luzon/Zambales Prov.	Mt. High Peak, Palauig Munic., Brgy. Salasa	HM371013
Apomys	*zambalensis*	FMNH 178288	Luzon/Zambales Prov.	Mt. High Peak, Palauig Munic., Brgy. Salasa	HM371014
Apomys	*zambalensis*	FMNH 178293	Luzon/Zambales Prov.	Mt. High Peak, Palauig Munic., Brgy. Salasa	HM371015
Apomys	*zambalensis*	FMNH 178296	Luzon/Zambales Prov.	Mt. High Peak, Palauig Munic., Brgy. Salasa	HM371016

Appendix I

Continued.

Genus	Species	Voucher	Island/Province	Locality	GenBank accession
Apomys	*zambalensis*	FMNH 178297	Luzon/Zambales Prov.	Mt. High Peak, Palauig Munic., Brgy. Salasa	HM371017
Apomys	*zambalensis*	FMNH 178310	Luzon/Zambales Prov.	Mt. High Peak, Palauig Munic., Brgy. Salasa	HM371018
Apomys	*zambalensis*	FMNH 178327	Luzon/Zambales Prov.	Mt. High Peak, Palauig Munic., Brgy. Salasa	HM371019
Apomys	*zambalensis*	FMNH 183348	Luzon/Bataan Prov.	0.7 km N, 0.2 km W Mt. Natib Peak	HM371020
Apomys	*zambalensis*	FMNH 183393	Luzon/Bataan Prov.	0.7 km N, 0.2 km W Mt. Natib Peak	HM371021
Apomys	*zambalensis*	FMNH 183395	Luzon/Bataan Prov.	0.7 km N, 0.2 km W Mt. Natib Peak	HM371022
Apomys	*zambalensis*	FMNH 183405	Luzon/Bataan Prov.	0.3 km N, 0.1 km W Mt. Natib Peak	HM371023
Apomys	*zambalensis*	FMNH 183407	Luzon/Bataan Prov.	0.3 km N, 0.1 km W Mt. Natib Peak	HM371024
Apomys	*zambalensis*	FMNH 183414	Luzon/Bataan Prov.	0.1 km N Mt. Natib Peak	HM371025
Apomys	*zambalensis*	FMNH 183530	Luzon/Zambales Prov.	Palauig Munic.: Brgy. Salasa: Mt. Tapulao	HM371026
Apomys	*zambalensis*	FMNH 183532	Luzon/Zambales Prov.	Palauig Munic.: Brgy. Salasa: Mt. Tapulao	HM371027
Apomys	*zambalensis*	FMNH 183535	Luzon/Zambales Prov.	Palauig Munic.: Brgy. Salasa: Mt. Tapulao	HM371028
Apomys	*zambalensis*	FMNH 183537	Luzon/Zambales Prov.	Palauig Munic.: Brgy. Salasa: Mt. Tapulao	HM371029
Apomys	*zambalensis*	FMNH 183539	Luzon/Zambales Prov.	Palauig Munic.: Brgy. Salasa: Mt. Tapulao	HM371030
Apomys	*zambalensis*	FMNH 183604	Luzon/Bataan Prov.	0.7 km N, 0.2 km W Mt. Natib Peak	HM371031
Apomys	*zambalensis*	FMNH 183610	Luzon/Bataan Prov.	0.7 km N, 0.2 km W Mt. Natib Peak	HM371032
Apomys	*zambalensis*	FMNH 183617	Luzon/Bataan Prov.	0.3 km N, 0.1 km W Mt. Natib Peak	HM371033
Apomys	*zambalensis*	FMNH 183618	Luzon/Bataan Prov.	0.3 km N, 0.1 km W Mt. Natib Peak	HM371034

Chapter 2: Mammalian Diversity Patterns on Mount Palali, Caraballo Mountains, Luzon

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Abstract

In 2005 and 2007, we conducted surveys of mammals along an elevational transect on Mount Palali (peak 1707 m) in the Caraballo Mountains, a poorly known mountain range on Luzon Island, Philippines. The surveys covered eight localities representing habitats from lowland agroforest and regenerating disturbed lowland rainforest at 780 m to mossy forest near the peak. We recorded 24 species, including one native shrew, one non-native shrew, five fruit bats, seven insectivorous bats, one monkey, six native rodents, two civets, and one pig. One species of *Apomys* is the newly described *A. sierrae,* and two species of *Chrotomys* are potentially undescribed species. Elevational patterns varied among mammals: bats were most diverse in the lowlands, native nonvolant small mammals had almost equal richness along the entire elevational transect, and most species of large mammals were present at all elevations. Bait attractiveness and diel activity pattern differed among native nonvolant small mammals: *Apomys microdon* and *Rattus everetti* were nocturnal and attracted to coconut baits, *Chrotomys* sp. 1 and 2 were mostly nocturnal and favored earthworms, *Crocidura grayi* showed no bait preference and was active during day and night, and *A. sierrae* showed no bait preference and was most active at night. The non-native *Suncus murinus* was restricted to highly disturbed areas at 780 m, whereas all native nonvolant small mammals were present in both degraded and undisturbed forest, supporting the hypothesis that non-native small mammals are not successful in invading native habitats on oceanic islands when the native community of small mammals is diverse. We conclude that all three rainforest types at all elevations, including newly regenerating forest, provide important habitat for mammals on Mount Palali.

Introduction

The terrestrial mammals of the Philippine archipelago constitute one of the most remarkable assemblages in the world for having a high level of species richness (ca. 183) and a high proportion of endemics (ca. 66%; Heaney et al., 1998; Catibog-Sinha & Heaney, 2006). A substantial part of this diversity and endemism is attributed to the archipelago's complex geologic history (Hamilton, 1979; Hall, 1998; Yumul et al., 2008), which had a profound effect on the evolutionary processes that gave rise to a highly diverse and distinctive set of mammals (Heaney & Regalado, 1998; Steppan et al., 2003; Jansa et al., 2006; Esselstyn et al., 2009). Most of the islands are volcanic in origin and have had no dry-land connection to the Asian continent throughout their geological lifespan (Heaney, 1986; Hall, 1998). Previous surveys have shown that each major island (or set of closely adjacent islands that were connected to each other during the last glacial maximum) is a unique center of mammalian diversity, with levels of endemism ranging from 40% to nearly 90% (Heaney, 1986; Heaney & Regalado, 1998; Catibog-Sinha & Heaney, 2006; Balete et al., 2009). Additionally, each major island has a unique history of geologic processes that resulted in isolated mountain ranges and peaks of differing elevation. On Luzon Island, the oldest and largest island in the country at 108,000 km^2, the landscape is characterized by several mountain ranges and isolated massifs, such as the Central Cordillera of northern Luzon, the northern Sierra Madre of northeastern Luzon, the Mingan Mountains of the central Sierra Madre, the Zambales Mountains of west-central Luzon, and Mount Isarog in southern Luzon (see fig. 3 in Heaney et al., this volume). Each of these areas has been shown to harbor a distinct set of mammals and each is recognized as a subcenter of mammalian endemism (Rickart et al., 1991; Heaney et al., 1999; Ong et al., 2002; Heaney et al., 2003; Duya et al., 2007; Balete et al., 2009, this volume). Additional mountain ranges and isolated peaks on Luzon are part of our ongoing effort to locate and document all of the subcenters of endemism (e.g., Balete et al., 2009; Rickart et al., 2011).

This paper constitutes the first documentation of the ecology and diversity patterns of mammals on another mountain range on Luzon, the Caraballo Mountains. In conducting our surveys, we established an elevational transect from 780 to 1707 m on Mount Palali, the highest peak in the Caraballos at 1707 m, with three primary objectives in mind: 1) determine which species of mammals are present, 2) describe their patterns of distribution along the elevational transect, and 3) document the habitat associations of each species. We also provide ecological information for the newly described *Apomys sierrae* (Heaney et al., this volume) and two potentially undescribed species of *Chrotomys* (E. A. Rickart, unpubl. data) that we captured on Mount Palali, herein referred to as *Chrotomys* sp. 1 and sp. 2.

In the course of our surveys, we also gathered data relevant to two patterns of mammalian distribution, particularly nonvolant small mammals, on Philippine mountains. First, previous studies of small mammals along elevation gradients have documented a consistent pattern of increasing species richness and relative abundance with increasing elevation up to about 2000 m; when the mountain reaches only this elevation, species richness reaches its maximum near this elevation (Heaney et al., 1989, 1999, 2006b; Rickart et al., 1991, 1993; Heaney, 2001; Balete et al., 2009, this volume). On higher mountains, such as Mount Kitanglad (Mindanao Island), species richness and relative abundance peak at about 2000–2200 m and then decline steadily above this level, producing a curvilinear pattern (Heaney, 2001; Heaney et al., 2006b). Our results for Mount Palali, which is a relatively low mountain, are presented here and will be synthesized with other data in other publications as a test of the general pattern (e.g., Rickart et al., 2011).

We also gathered data on Mount Palali to test a second hypothesis: that the number of species in the native community of small mammals determines the success of non-native small mammals in invading native habitats on oceanic islands (Heaney et al., 1999). This hypothesis is based on a pattern documented on six mountains of the Philippines: Mount Isarog (Heaney et al., 1999), Mount Tapulao (Balete et al., 2009), and Mt. Bali-it, Balbalasang (Rickart et al., 2011), on Luzon; Mount Guinsayawan on Negros Island (Heideman et al., 1987; Heaney et al., 1991); Mount Timpoong on Camiguin Island (Heaney et al., 2006a); and Mount Pangasugan on Leyte Island (Rickart et al., 1993).

Methods

Study Area

At 1707 m, Mount Palali (peak at 16°25′40″N, 121°13′17″E) is the highest point in the Caraballo Mountains. The Caraballos lie within the provinces of Nueva Vizcaya, Nueva Ecija, and Quirino and lie between the southern tip of the Central Cordillera to the west and the middle portion of the Sierra Madre to the east, forming a connection between the two mountain ranges. The Caraballos constitute a volcanic center of Pliocene–Pleistocene origin, part of a volcanic belt complex of the Santa Ana Volcanic Belt–Luzon Central Cordillera Belt–Central Luzon Belt–Cuyo Belt (Vasquez et al., 1997; Yumul et al., 2008), one of the many belts in the Philippines that gave rise to thermal areas that have been explored previously for geothermal power sources (Malapitan & Reyes, 2000). Copper deposits of the Kuroko type associated with andesitic flows and pyroclastic material are found within the mountain range about 10 km northeast of Mount Palali and are currently being mined (Mines and Geoscience Bureau, 2005).

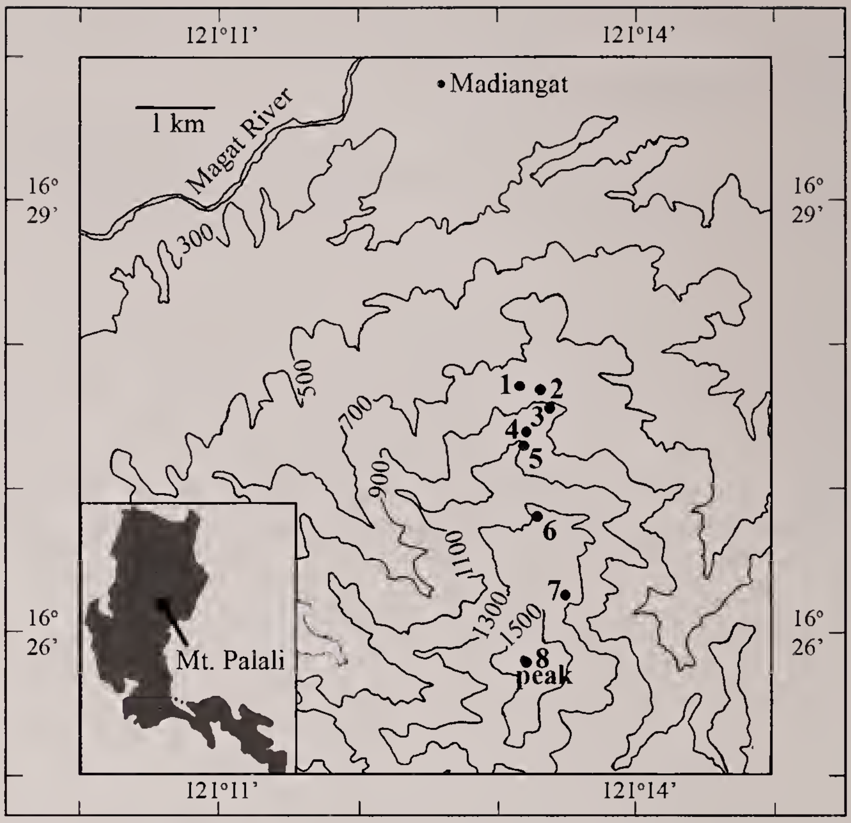

Fig. 1. Map of Mt. Palali, showing the location of study localities in 2005 (7 and 8 only) and 2007 (all), numbered as in text. Inset map of Luzon Island shows location of Mt. Palali.

In contrast to the geological resources, the Caraballo biota is poorly known. The mountain range has been designated as one of the 19 biodiversity corridors in the Philippines and recognized as a high-priority area for research and conservation (Ong et al., 2002). No detailed biological inventories of mammals have been done in the Caraballo mountains, although Dalton Pass at Sta. Fe, Nueva Vizcaya Province (50 km southeast of Mount Palali), was the site of an extensive bird-banding survey under the Migratory Avian Pathogen Survey (MAPS) program from 1964 to 1971 (McClure & Leelavit, 1972). Among mammals, Heaney et al. (1998, 2000) reported only 10 species of mammals (with specimens deposited in museums) within the three provinces (Nueva Vizcaya, Nueva Ecija, and Quirino) where the Caraballo Mountains lie. These were seven bats (*Desmalopex leucopterus*, *Otopteropus cartilagonodus*, *Ptenochirus jagori*, *Pteropus hypomelanus*, *Taphozous melanopogon*, *Hipposideros diadema*, and *Myotis rufopictus*) and three murid rodents (*Chrotomys mindorensis*, *Phloeomys pallidus*, and *Rattus norvegicus*).

The vegetation on the northern side of Mount Palali, where the fieldwork was concentrated, consisted of several types: "parang" grassland, agroforest, mature and regenerating (previously logged over) lowland dipterocarp forest, mature montane forest, and mature mossy forest. The trail we followed leading to Mount Palali (an old logging road) started at the village of Madiangat (Quezon Municipality, Nueva Vizcaya Province), where most of the residences are concentrated (Fig. 1). Situated near the houses were farm lands consisting mostly of rice fields and corn plantations and an occasional citrus orchard. Beyond the lowland farms, parang grassland dominated much of the lowland areas of the mountain starting from ca. 300 m and extending along the rolling landscape of deep ravines and steep hills and ridges up to ca. 650 m. Within this expanse of grassland were isolated stands of banana (*Musa* spp.), mango (*Mangifera indica*), and

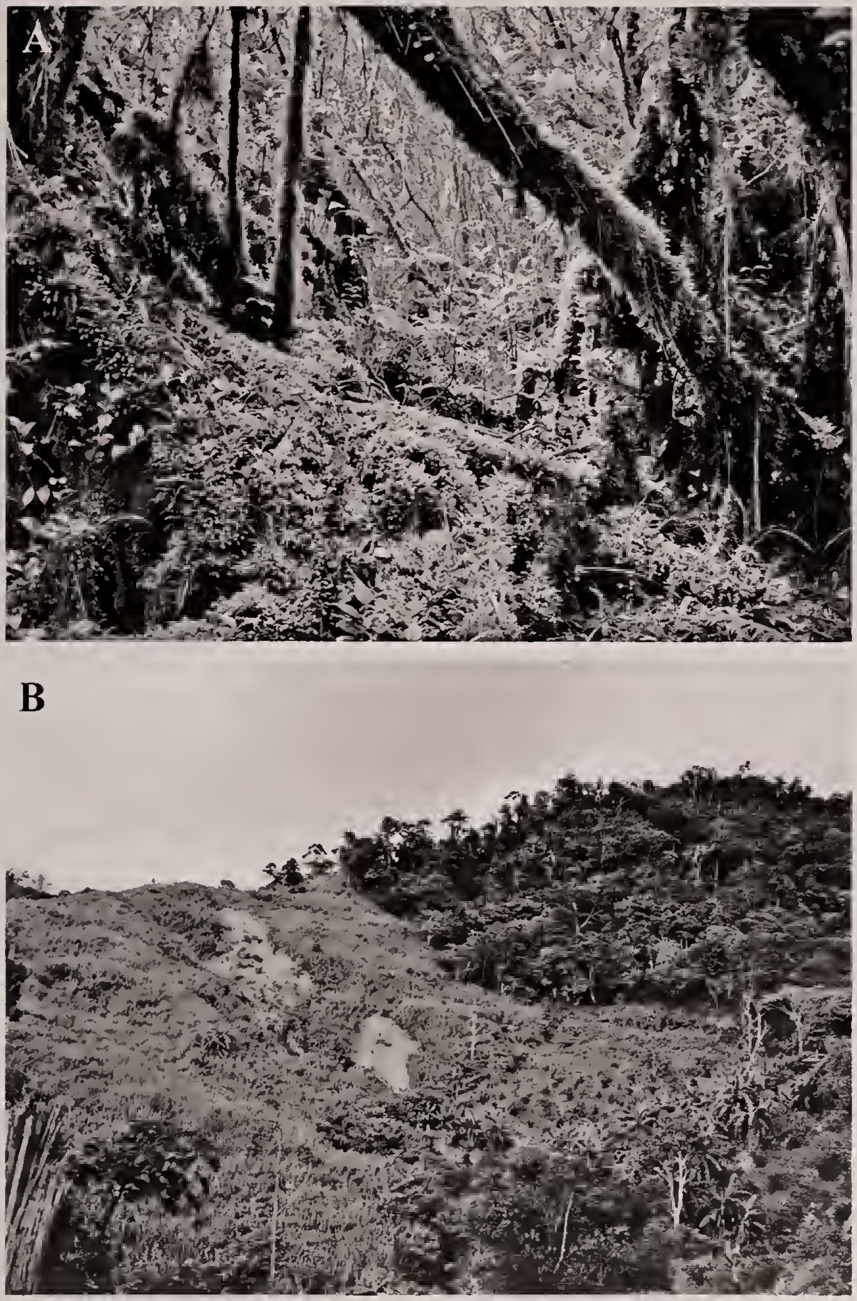

Fig. 2. Habitats on Mt. Palali showing (**A**) mossy forest habitat near the summit of Mt. Palali at locality 8, 1707 m elevation. March 2007, M. R. M. Duya; (**B**) Highly disturbed mixture of regenerating second-growth lowland forest, agricultural areas, and grassland at locality 1 at 780 m elevation. This is the elevation at which forest began. March 2007, M. R. M. Duya.

erect bamboo (*Schizostachyum* spp.), which were usually found along hillsides of moderate slope. We observed flowing water in some of the ravines, but most have pipe systems draining them, presumably for household water supply and irrigation for rice and corn. The forest line started above 750 m with vegetation that was mainly a mixture of highly disturbed second-growth lowland forest, citrus orchards, and mangoes, although there were signs of regeneration, with saplings 10–20 cm in diameter at breast height (DBH) common along the trail. Areas of slash-and-burn farming (*kaingin*) were common near the lower forest line. Between 800 and 950 m, regenerating lowland forest was more extensive, although a large area of *kaingin* was seen at 900 m. The old logging road began to narrow at the end of the *kaingin,* becoming a trail that continued its way upward toward the peak. From 1000 to 1400 m, montane forest occurred on the sides of undisturbed steep ridges and ridge tops. Between 950 and 1050 m, two separate landslides were seen that were possibly caused by large amounts of precipitation produced by typhoons. Primary mossy forest occurred from 1400 m up to the peak at 1707 m. Except for our campsite at 1420 m, no signs of disturbance were seen within the mossy forest.

Our surveys were conducted during two separate field seasons at eight elevational localities (Fig. 1), enumerated and described below, all within Barangay Madiangat, Quezon Municipality, Nueva Vizcaya Province. The first took place from 13 to 22 September 2005, and the second from 5 to 29 March 2007. The first survey sampled at 1420 m and near the peak (1707 m; localities 7 and 8, below). Nonvolant small mammal trapping was done at both elevations, whereas netting was confined to 1420 m. During the second survey, an elevational transect was established, covering the entire elevational range of Mount Palali, and the 1420- and 1707-m localities were resampled. Overall, we sampled in habitats that included agroforest and highly disturbed lowland dipterocarp forest (localities 1 and 2, at 780 and 800 m), good-quality regenerating lowland dipterocarp forest (locality 3, 900 m), transitional lowland/lower montane forest (locality 4, 1040 m), old-growth montane forest (localities 5 and 6, 1100 and 1300 m), and lower and upper mossy forest, including the peak (localities 7 and 8, 1420 and 1707 m).

Locality 1—3.3 km N, 0.5 km W of Palali peak, 780 m elev., 16°27′43.7″N, 121°13′06.9″E (22–25 March 2007). This locality was situated in a highly disturbed mixture of second-growth lowland forest and agricultural areas and was where the forest line began (Fig. 2B), in the form of regenerating second-growth lowland forest. This area had been partially logged in the early 1980s but had regenerated by the time of our survey. A mosaic of citrus orchards and occasional fruit trees (e.g., mangoes) and pastures was present below the forest line and at least two *kaingin* areas planted with root crops were present in the forest interior. The vegetation within the forest consisted mostly of figs (*Ficus* spp.), other nontimber trees, and regenerating saplings with DBH ranging from 5 to 10 cm. Dipterocarps were present but rare and were among the tallest emergents, reaching heights of ca. 25 m. Canopy height, for the most part, reached ca. 20 m, with DBH not exceeding 50 cm. Canopy vines were common, particularly climbing bamboo (*Dinochloa* spp.) that hung between trees. Epiphytes consisted chiefly of aroids and ferns. Aside from tree saplings, forest floor vegetation consisted of rattans (*Calamus* spp.) and herbaceous plants such as gingers (*Zingiber* spp.), ferns (*Diplazium* spp.), tree ferns (*Cyathea* spp.), and erect pandans (*Pandanus* spp.). Leaf litter on the floor was light, with accumulations of 2–3 cm around tree trunks, and scattered patches of humus did not exceed 2 cm depth. Our total sampling effort at this locality consisted of 20 net-nights, seven V-net-hours (see Trapping Procedures), and 498 trap-nights.

Locality 2—3.25 km N, 0.2 km W of Palali peak, 800 m elev., 16°27′41.9″N, 121°13′16″E (18–21 March 2007). Sampling at this locality was conducted in lowland forest that had been partially logged previously but had regenerated relatively well compared with locality 1. Saplings were thicker (DBH = 10–15 cm) and in some instances reached heights of 15–20 m. The canopy and emergents were mainly dipterocarps and other timber-quality trees, with heights reaching 25–35 m. Canopy and emergent trees had greater DBH than at locality 1, with many ranging from 75 to 100 cm. Trees with DBH exceeding 100 cm were present but uncommon. Old stumps of wide-girthed canopy trees were evident, especially along the old logging road. Forest floor vegetation was similar to locality 1, comprising mainly tree saplings, rattans, ferns, and aroids. Canopy vines were common, comprising mainly climbing bamboo and strangling figs, whereas epiphytes (also common) consisted of ferns, aroids, and orchids. Sampling at this locality was limited to mist netting, with an effort of six net-nights.

Locality 3—3.05 km N, 0.1 km E of Palali peak, 900 m elev., 16°27′34.3″N, 121°13′19″E (18–21 March 2007). Sampling at this locality was conducted at the end of the road that narrowed to a trail leading directly to the peak. Vegetation along the old logging road was of secondary lowland dipterocarp forest similar to locality 2. This homogeneous vegetation of second-growth forest, which started from locality 2, was abruptly interrupted by a wide expanse of an old *kaingin* farm planted with abaca (*Musa*) and corn. At that point, the logging road ended and was replaced by a trail that entered a regenerating forest of good quality that had been lightly disturbed. Within this vegetation, emergent trees reached heights of 30–40 m and were dominated by species of Dipterocarpaceae, Fagaceae, and the large-buttressed *Dracontomelon* (Anacardiaceae). Canopy trees with heights of 25–30 m were common at this locality, with DBH of 100–150 cm. Canopy vines such as climbing bamboo were common, as were epiphytes such as orchids and ferns. Rattan vines were more abundant than at localities 1 and 2. Most of the forest floor vegetation was dominated by herbaceous plants such as gingers, ferns, and other shrubs (e.g., *Donax*). Small saplings were less common. Instead, there were trees of DBH exceeding 20 cm. Leaf litter was nearly continuous but did not exceed 4 cm thickness, and humus depth was similar to locality 2. Our total sampling effort consisted of 15 net-nights and 530 trap-nights; nets at this locality were maintained concurrently with those at locality 2.

Locality 4—2.75 km N, 0.3 km W of Palali peak, 1040 m elev., 16°27′24.1″N, 121°13′10″E (25–28 March 2007). This locality was in transitional lowland/lower montane forest along the northern slope at 1000–1100 m elevation. The slope was steep and the ground was covered with abundant leaf litter. Sampling was mainly done along the slope and at the top of a ridge that was relatively flat. The vegetation consisted mostly of small trees with DBH of 15–25 cm and a few large trees standing 25–30 m with 40–50 cm DBH; trees with height of 20–25 m, mostly oaks (*Lithocarpus* spp.), were common. Tree trunks and branches covered with moss began to become common at this elevation. Tree ferns (*Cyathea* spp.) were common. Vines and epiphytes such as ferns, rattan, orchids, climbing bamboo, and aroids clung to most of the emergent and canopy trees. Humus was relatively more common and thicker than at localities 1, 2, and 3, but was mostly scattered. Forest floor vegetation consisted mainly of ferns and herbaceous plants such as gingers. Large boulders were present along the steep slope, and a portion of the ground was littered with rocks. A wide and steep landslide was present near the start of our trap-line, culminating in a ca. 50-m drop in elevation. Our total sampling effort at this locality consisted of three net-nights, 365 trap-nights, and three hours of V-netting.

Locality 5—2.6 km N, 0.1 km E of Palali peak, 1100 m elev., 16°27′18.5″N, 121°13′19″E (25–28 March 2007). This locality was situated in lower montane forest on a flat ridgetop about 500 m along the trail uphill from locality 4. We set a series of six mist nets along the flat and moderately wide (ca. 5 × 50 m) ridgetop, which was covered mostly with short grasses and a few stands of tree ferns. The sides of the ridge were steep and covered with trees of Myrtaceae, Fagaceae, and Lauraceae, with canopies reaching 15–20 m and DBH of 25–35 cm, although smaller trees (10–20 cm DBH) also were abundant. Lianas and canopy epiphytes (mainly ferns and mosses) were present, clinging to the canopy trees situated at the sides of the ridge. Only mist netting was done at this locality, with an effort of 18 net-nights.

Locality 6—1.75 km N, 0.1 km W of Palali peak, 1300 m elev., 16°26′48.7″N, 121°13′14″E (14–17 March 2007). This locality was situated in mature montane forest at 1240–1300 m. Sampling was done near the trail and perpendicular to it, traversing deep ravines and dry creeks. The trail near the locality was very steep (ca. 35–45°). The forest had a fairly low canopy, usually 17–20 m, mostly consisting of Fagaceae, Lauraceae, and Myrtaceae; the height of emergent trees was usually 20–25 m, and DBH was 15–25 cm, although a few trees were 30–35 cm. Epiphytes were abundant, including ferns, orchids, and mosses. Moss growth on tree trunks and branches had increased considerably from that seen at localities 4 and 5. Arborescent pandans (*Pandanus* sp.), shrubs (e.g., *Melastoma* spp.), and tree ferns (*Cyathea* spp.) were common, and climbing pandans (*Freycinetia* spp.) were abundant. Leaf litter and humus were thicker than at the lower localities, at ca. 10–12 cm and 10–15 cm depth, respectively; fallen (and rotting) logs were occasionally encountered. There were no signs of human disturbance. Our sampling effort consisted of 465 trap-nights; netting was not conducted.

Locality 7—0.8 km N, 0.55 km E of Palali peak, 1420 m elev., 16°26′16″N, 121°13′29″E (14–22 September 2005 and 8–16 March 2007). Sampling at this locality was conducted in mossy forest. The locality was on relatively flat ground northeast of Mount Palali peak in terrain interrupted by small streams and dry creek-beds on the saddle of the mountain. The height of the canopy was usually 8–10 m with DBH of 15–20 m, although trees of less than 15 cm were present. Gymnosperms, mostly species of *Dacrydium*, were among the tallest and thickest trees, reaching heights of 12–18 m and 30–40 cm DBH. Oaks, laurels, tree ferns, and arborescent *Pandanus* were common. Epiphytes were abundant, including mosses, ferns (e.g., *Asplenium*), and orchids. Canopy vines such as *Freycinetia* spp. were abundant. The ground off the trail was covered by abundant and thick leaf litter atop deep humus. Moss covered nearly all tree trunks, branches, and fallen logs and often covered some of the ground; virtually all mosses were water-soaked. Sampling effort during the 2005 survey was 955 trap-nights and four net-nights; sampling in 2007 consisted of 478 trap-nights, 41 net-nights, and three hours of V-netting.

Locality 8—Palali peak, 1707 m elev., 16°25′39.9″N, 121°13′17″E (17–22 September 2005 and 8–11 March 2007). Sampling at this locality was concentrated near the peak in mossy forest (Fig. 2A). The peak is about 1 km from locality 7 and was connected to it by a well-traveled trail. Approximately halfway along the trail toward the peak, the slope became very steep (ca. 40–45°) and continued to be steep until reaching the outside perimeter of the peak, which was relatively flat. Vegetation structure at this locality was similar to locality 7, although canopy and emergent heights were reduced, at 5–6 m and 9–10 m, respectively; most of the vegetation was between 3 and 5 m. Tree girths also were smaller, about 8–12 cm, and 30–40-cm DBH trees were rare. Most of the trees, represented by Myrtaceae, Fagaceae, Lauraceae, Elaeocarpaceae, and Vacciniaceae, were leaning, possibly resulting from heavy winds. Trees belonging to

Dacrydium were among the tallest species, although they were shorter than those at locality 7. Epiphytes were abundant, mostly consisting of orchids, ferns, and mosses, whereas climbing pandan (*Freycinetia* spp.) and climbing bamboo (*Schizostachium* spp.) formed complicated criss-crossing networks that clung to the canopy. Moss growth was ubiquitously present on tree trunks, branches, ground, and fallen trees. Leaf litter and humus were abundant, particularly off the trail. Sampling effort during the 2005 survey was 521 trap-nights, and sampling effort in 2007 consisted of 487 trap-nights and 21 net-nights.

Trapping Procedures

To make comparisons possible among localities along this transect of Mount Palali and with transects on other Philippine mountains, our methods followed the same procedures used previously (Heaney et al., 1989, 1991, 1999, 2006a,b; Rickart et al., 1991, 1993, 2011; Balete et al., 2009).

For bats, we used mist nets with an average mesh size of 36 mm and height and length of 2.5 and 12 m. Mist nets were set in areas of "bat traffic," such as ridgetops and across trails and streams in forest, and among fruit trees in agroforest areas. Mist netting stations (or net-lines) consisted mostly of a series of two to five mist nets, depending on the availability of space; in some cases, nets were set singly. On most nights, net-lines were tended continuously during the primary activity peak from early dusk to about 2000 h and were checked afterward every 30 minutes until 2200 h; nets were left open thereafter, and bats were removed at dawn. Nets were left in place for three to four consecutive nights. In addition to mist netting, we also employed a new technique called V-netting (Duya et al., 2007) to capture insectivorous bats. V-nets were set along trails and narrow creeks and tended at dusk for one hour; V-nets were then closed afterwards. Similar to mist nets, V-nets were operated for three to four consecutive days. Mist nets were set at all sampling localities (localities 1–8), whereas V-netting was done at three (localities 1, 4, and 6) of the eight sampling localities.

We used Victor rat traps and Museum Special snap traps to capture non-volant small mammals (i.e., rodents and shrews) within an elevational band of ±50 m at six (localities 1, 3, 4, 6, 7, and 8) of the eight sampling localities. For trapping on the ground surface, traps were placed in various suitable situations, including under root tangles, in front of burrow entrances, along runways, and on top of or beside fallen logs. Traps were baited with either live earthworms (Megascolecidae) or fried coconut coated with peanut butter. Earthworms were affixed to bait pedals of traps by small safety pins. For aboveground trapping, Museum Specials were set on horizontal branches of trees, crisscrossing vines of climbing pandan (*Freycinetia* spp.) or climbing bamboo (*Dinochloa* spp.), or overhanging lianas; all arboreal traps were baited with fried coconut coated with peanut butter. Ground traps (solely Victor snap traps) composed 94% of traps set, whereas arboreal traps (Victors and Museum Specials) represented 6%; traps baited with coconut constituted 64% of the traps set, whereas 36% were baited with earthworms. Individual trap-lines of 30–50 traps typically were operated for three days and serviced twice each day, early in the morning (after sunrise, ca. 0700 h) and in the late afternoon (before sundown, ca. 1700 h) to retrieve captures and replace bait. Within each locality where trapping was done, we sampled various microhabitats, such as ridgetops, sides of ridges, and along trails and creeks.

Information on the presence and perceived abundance of large mammals, including cloud rats, macaques, civets, and wild pigs, was obtained from direct and indirect (e.g., fecal matter and wallows) observations and from knowledgeable local guides and hunters encountered during field work.

Voucher specimens were preserved for all species that were trapped or netted; all were cataloged and studied at the Field Museum of Natural History (FMNH), and a portion will be transferred to the National Museum of the Philippines, Manila (NMP). Almost all specimens were preserved in formalin in the field; these were injected with an unbuffered, saturated solution of formalin, then placed in a 10% formalin solution to which a small amount of soap had been added to allow the formalin to penetrate to the skin. After several weeks, they were thoroughly rinsed in water, then transferred to ethanol for permanent storage. Some skulls were subsequently removed and cleaned so that representatives could be used in taxonomic studies. Tissue samples for genetic studies were taken from fresh specimens. Specimens that were not preserved in formalin were prepared as skeletons and stored in 70% ethanol, then cleaned for study at FMNH.

Specimens that were prepared as skeletons were examined in the field for reproductive status; those preserved in formalin were examined in the museum. Embryo size was measured as crown-to-rump length (CRL). Uterine scars were detected as dark areas of pigment. Nipples were recorded as enlarged (having nursed young) or small (not having nursed). Multiparous females were defined as those showing evidence of enlarged nipples and uterine scars; females that were pregnant but had small nipples were considered as primiparous. Nulliparous females were small, nonbreeding individuals with small nipples and lacking uterine scars. For male specimens, we recorded testes position (abdominal or scrotal) and size (length and width).

Standard external measurements (total length, tail vertebrae, forearm, hind foot including claw, and ear) and weight (in grams) were taken in the field on fresh specimens. The nomenclature of mammals used here follows Heaney et al. (1998). The capture and handling of animals in the field was conducted in accordance with all Philippine laws and regulations.

Data Analysis

Adequacy of sampling was assessed by calculating species accumulation rates for each sampling locality and for the transect as a whole. This is the best indicator of the completeness of sampling for species richness of small mammals in any place pre-existing information is limited or absent, as in much of the Philippines (Rickart et al., 1991; Heaney et al., 1999, 2006b; Heaney, 2001; Balete et al., 2009). Accumulation curves were prepared solely for native non-volant small mammals; accumulation curves were not constructed for bats because we assume incomplete sampling due to low sampling effort. Large mammals were excluded as well because effort in recording them was not standardized.

Results of the survey included those individuals that were released. In 11 cases (3 in fruit bats, 7 in insectivorous bats, and 1 in non-volant small mammals), we inferred the presence of a particular species at a given locality because of its documented presence at localities above and below along the transect (Rickart et al., 1991).

For bats, our measure of relative abundance is expressed as netting success and calculated as the number of captures at a given locality divided by the number of net-nights (for mist nets) or net-hours (for V-nets). Relative abundances of fruit bats were derived from relevant mist netting effort; depending on which method was used, relative abundances of insectivorous bats were computed from either mist netting or V-netting effort. Because our effort to sample insectivorous bats was low and uneven, we conducted no statistical tests of patterns; instead, we simply report our captures, which add to a growing body of data about these poorly known species.

For murid rodents and shrews, we report the total number of trap-nights (defined as 1 trap set for 24 hours), the number of traps placed on the ground with earthworm or coconut bait, and the number of traps with coconut bait placed arboreally. Trap success was derived for each study locality by bait type as the number of individuals of each species captured with the relevant bait divided by the corresponding number of trap-nights that the bait was used times 100 (i.e. the number of captures per 100 trap-nights). Bait preference of each species was derived in a similar manner, expressed as the value of their total captures per bait type divided by the relevant total of trap-nights for the bait used times 100. Overall trap success weighted by bait type at each locality was calculated as the number of individuals captured divided by the total number of trap-nights (either on the ground or in the trees, depending on whether the species is terrestrial or arboreal) times 100. Thus, for *Chrotomys* spp., which live only on the ground, we did not include arboreal traps in this calculation. The unweighted (i.e., equalized) value of the same parameter was expressed as the average of trap success for each species for the two bait types used. Because the unweighted value is independent of bait type, we consider it to be our most meaningful and consistent measure for any comparisons. We use the term "relative abundance" because it is expressed as the number of captures per unit of effort, rather than a measure of abundance expressed as number of individuals per unit of area.

G-tests were used to determine significant variation in the distribution (measured by relative abundance) of species (both fruit bats and native nonvolant small mammals) across the elevational transect. To determine elevation preference of each species, χ^2 tests were employed, using the relevant number of net-nights (for fruit bats captured in mist nets) or trap-nights (for nonvolant small mammals). This was done by comparing capture rates between paired forest localities; for fruit bats, only the lowland forest pair (780 and 900 m) and mossy forest pair (1420 and 1707 m) were compared because of low sampling effort in our montane forest localities (1040 and 1100 m); for native murids and shrews, pairs of lowland (780 and 900 m), montane (1040 and 1300 m), and mossy (1420 and 1707 m) forest localities were compared with one another. χ^2 tests were employed to determine bait preference and diel activity. For diel activity, the expected frequency is computed as the ratio 10:14, the proportion (in 24 hours) between diurnal and nocturnal/crepuscular activity. For all χ^2 tests, we followed the convention of conducting tests only on total samples of 20 or more individuals, with five or more individuals per "treatment" in at least 80% of the treatments (e.g., per elevation or bait type). Spearman's rank correlation (r_s) was used to determine the correlation of various parameters (e.g., species richness and relative abundance) with elevation. All test statistics were appraised at a minimum 0.05 level of significance, computed using Excel. The non-native *Suncus murinus* was not included in the G- and χ^2 tests, nor in the rank correlation analysis.

Numerical estimates were not possible for large mammals; rather, we recorded only presence or absence. Data presented here were based on reports from local guides and hunters and presence of sign (e.g., feces and wallows).

Results

Our survey documented 24 species of mammals on Mount Palali, consisting of one native shrew plus one non-native shrew, five fruit bats, seven insectivorous bats, six native murid rodents (including *Phloeomys pallidus*, which we treat as a large mammal because they weigh more than 2 kg and are hunted), one macaque, two civets, and one warty pig.

The large-bodied *Apomys* from Mt. Palali has been described as *A. sierrae*, which occurs from the northernmost tip of the Sierra Madre to Mt. Palali (Heaney et al., this volume). Our preliminary taxonomic studies indicate that the species we refer to as *Chrotomys* sp. 1 and 2 might represent previously undescribed species; taxonomic studies are ongoing (E. A. Rickart, unpubl. data).

Adequacy of Sampling

Before interpreting the field data, it is necessary to evaluate the extent to which these data are complete and reliable. In doing so here, we follow the procedures used by Heaney et al. (1989, 1991, 1999, 2006a,b), Rickart et al. (1991, 1993), and Balete et al. (2009).

Fruit Bats—Heaney et al. (1998) reported four species of fruit bats within the provinces that include Mount Palali and the Caraballo Mountains. This included two small (*Otopteropus cartilagonodus* and *Ptenochirus jagori*) and two large (*Desmalopex leucopterus* and *Pteropus hypomelanus*) fruit bats. Our netting effort of 128 net-nights yielded five species, all small fruit bats (Table 1); we did not document the presence of any large fruit bats. Including our survey results, the number of fruit bat species known for the Caraballo Mountains stands at seven. Nonetheless, we consider our effort to be insufficient to fully document species richness on Mount Palali. At least 10 species of small fruit bats are found on Luzon Island; we did not capture five of these: *Eonycteris spelaea*, *E. robusta*, *Rousettus amplexicaudatus*, *Dyacopterus rickarti*, and *Harpyionycteris whiteheadi*. *Eonycteris spelaea* and *R. amplexicaudatus* are common and widespread, but the other three are poorly known and rarely captured in surveys despite extensive netting (Heaney et al., 1998, 1999, 2003; Duya et al., 2007).

Insectivorous Bats—Insectivorous bats use sophisticated sonar systems to navigate and hunt prey. They are thus difficult to capture in mist nets and have been underrepresented in mammal surveys in the Philippines (Heaney et al. 1998, 2003, 2006a,b; Sedlock, 2001, 2002; Duya et al., 2007; Sedlock et al., this volume). During our surveys, mist netting effort was augmented with V-netting to capture insectivorous bats (see Methods). We captured a total of 70 individuals representing seven species (Table 2); six species were captured with V-nets and four species in mist nets. Despite the use of two methods of capture, sampling effort was not extensive,

TABLE 1. Number of mist net captures of small fruit bats along the elevational transect on Mt. Palali, Luzon Island. Captures per net-night are in parentheses. The total number of species is the number documented plus those inferred to be present. Probabilities are for χ^2 tests comparing captures in lowland (780 and 900 m) and mossy (1420 and 1707 m) forest pairs with expected frequencies on the basis of relevant number of net-nights; localities 2, 4, and 5 are excluded in analysis because of low sampling effort. Locality pairs with captures greater than expected are designated by boldface. See Methods for details.

	No. of mist-net captures by locality (per net-night)							
Species	**1 780 m**	**2 800 m**	**3 900 m**	**4 1040 m**	**5 1100 m**	**7 1420 m**	**8 1707 m**	**Total**
Cynopterus brachyotis	4 (0.20)	4 (0.67)	3 (0.20)	0	0	0	0	11
Haplonycteris fischeri	2 (0.10)	1 (0.17)	0	0	0	0	0	3
Macroglossus minimus	2 (0.10)	1 (0.17)	1 (0.07)	1 (0.33)	0	0	0	5
Otopteropus cartilagonodus	0	0	0	0	0	**5**[a] (0.11)	**41**[a] (1.95)	46
Ptenochirus jagori	2 (0.10)	0[b]	0[b]	0[b]	1 (0.06)	3 (0.07)	0	6
Total fruit bats	10	6	4	1	1	**8**[a]	**41**[a]	71
Total net-nights	20	6	15	3	18	45	21	128
Fruit bats per net-night	0.50	1.00	0.27	0.33	0.06	0.18	1.95	0.56
Total no. of species	4	3 + 1	2 + 1	1 + 1	1	2	1	5

[a] $P < 0.001$.

[b] Presence inferred (see Methods).

and V-netting was limited to only three localities. For this reason, we believe our species richness tally is likely to be quite incomplete and is not usable for estimates of species richness, as is often the case (Heaney et al., 2000). Our data, however, contribute to general knowledge of the natural history of these poorly known mammals.

NON-VOLANT SMALL MAMMALS—Our surveys documented seven species of non-volant small mammals on Mount Palali, consisting of two shrews (1 native and 1 non-native) and five native murid rodents (excluding *P. pallidus*, which we treat as a large mammal). We accumulated a total of 4299 trap-nights at six localities that included all major habitat types (lowland, montane, and mossy forest) on a typical Philippine mountain, yielding 266 captures. At these six localities, sampling was moderately to highly intensive, with a range of 365–1433 trap-nights per locality (Table 3). A species accumulation curve for the six native species documented during the entire survey (Fig. 3A) shows a rapid rise in the number of species at the

TABLE 2. Elevational distribution of insectivorous bats on Mt. Palali, Luzon Island, using mist nets and V-nets. Standardized captures per net-night and V-net hour are in parentheses; in each species' set of capture data, the first line of values corresponds to mist net captures and the second line corresponds to V-net captures. The total number of species for a locality is the number documented plus those inferred to be present.

		Distribution by locality							
Species	**Capture method**	**1 780 m**	**2 800 m**	**3 900 m**	**4 1040 m**	**5 1100 m**	**7 1420 m**	**8 1707 m**	**Total**
Hipposideros ater	Mist net	0	0[a]	0[a]	0	0	0	0	0
	V-net	2 (0.29)	—	—	1 (0.33)	—	0	—	3
Hipposideros diadema	Mist net	0	0	1 (0.07)	0	0	0	0	1
	V-net	0	—	—	0	—	0	—	0
Rhinolophus arcuatus	Mist net	1 (0.05)	0[a]	0[a]	0[a]	2 (0.11)	11 (0.24)	3 (0.14)	17
	V-net	0	—	—	0	—	5 (1.67)	—	5
Rhinolophus inops	Mist net	4 (0.20)	8 (1.33)	4 (0.27)	1 (0.33)	0[a]	0[a]	1 (0.05)	18
	V-net	7 (1.00)	—	—	4 (1.33)	—	0	—	11
Rhinolophus virgo	Mist net	0	0	0	0	0	0	0	0
	V-net	0	—	—	4 (1.33)	—	0	—	4
Kerivoula whiteheadi	Mist net	0	0	0	0	0	0	0	0
	V-net	0	—	—	1 (0.33)	—	0	—	1
Pipistrellus cf. *javanicus*	Mist net	0	0	0	0	0	5 (0.11)	4 (0.19)	9
	V-net	0	—	—	0	—	1 (0.33)	—	1
Total insectivorous bats		14	8	5	11	2	22	8	70
No. of insectivorous bats captured by mist net		5	8	5	1	2	16	8	45
Total net nights (bats per net-night)		20 (0.25)	6 (1.33)	15 (0.33)	3 (0.33)	18 (0.11)	45 (0.36)	21 (0.38)	114 (0.39)
No. of insectivorous bats captured by V-net		9	—	—	10	—	6	—	25
Total V-net hours (bats per V-net hour)		7 (1.29)	—	—	3 (3.33)	—	3 (2.00)	—	13 (1.92)
Total species of insectivorous bats		3	1 + 2	2 + 2	4 + 1	1 + 1	2 + 1	3	7
Total species of bats documented and inferred		7	7	7	7	3	5	4	12

[a] Presence inferred (see Methods).

TABLE 3. Elevational distribution of non-volant small mammals on Mt. Palali, Luzon Island. In each set of capture data, the number of captures is followed by the unweighted capture rate (per 100 trap-nights) in brackets. The total number of species is the number documented plus those presumed present. Probabilities are for χ^2 tests comparing number of captures of native mammals in lowland (780 and 900 m), montane (1040 and 1300 m), and mossy (1420 and 1707 m) forest pairs with expected captures based on relevant number of trap-nights. Locality pairs with captures greater than expected are designated by boldface.

Species	Distribution by locality						Total
	1 780 m	3 900 m	4 1040 m	6 1300 m	7 1420 m	8 1707 m	
Crocidura grayi[a]	0	1 [0.20]	0[d]	1 [0.22]	2 [0.15]	2 [0.22]	6
Suncus murinus[a,b]	2 [0.40]	0	0	0	0	0	2
Apomys sierrae[a]	18 [3.68]	21 [4.25]	16 [4.38]	20 [4.36]	66 [4.93]	42 [4.64]	183
Apomys microdon[c]	0	0	1	1 [0.04]	4 [0.01]	1	7
Chrotomys sp. 1[a]	**8**[e] [1.62]	**16**[e] [3.25]	2 [0.55]	1 [0.22]	**9**[e] [0.67]	**13**[e] [1.43]	49
Chrotomys sp. 2[a]	4 [0.83]	0	0	0	0	0	4
Rattus everetti[a]	3 [0.61]	2 [0.40]	2 [0.55]	1 [0.22]	7 [0.52]	0	15
Total captures	35	40	21	24	88	58	266
No. of ground trap-nights, coconut bait (captures)	250 (20)	249 (24)	213 (17)	254 (15)	1015 (51)	523 (24)	2504
No. of ground trap-nights, earthworm bait (captures)	239 (15)	244 (16)	152 (3)	205 (8)	324 (33)	383 (33)	1547
No. of arboreal trap-nights, coconut bait (captures)	9 (0)	37 (0)	0 (1)	6 (1)	94 (4)	102 (1)	248
Total ground trap success	7.16	8.11	5.48	5.01	6.27	6.29	—
Equalized ground trap success (averaged over bait types)	7.16	8.10	4.98	4.91	7.60	6.61	—
Total no. of native small mammal species	4	4	4 + 1	5	5	4	6

[a] χ^2 tests and capture rates based on ground traps only.

[b] Non-native species.

[c] Capture rates based on arboreal traps only; specimen at 1040 m captured by hand.

[d] Presence inferred (see Methods).

[e] $P < 0.001$.

start of trapping (5 species in ca. 700 trap-nights) followed by a brief plateau, with a rise to six species at about 1400 trap-nights. No further species were captured from 1400 to nearly 4300 trap-nights. Species accumulation curves for some individual localities (Fig. 3B) also showed some evidence of reaching plateaus. The accumulation curve for locality 7 (1420 m), where sampling was most extensive, reached a plateau at 700 trap-nights, with no species added up to 1400 trap-nights. At 1707 m (locality 8), the accumulation curve shows two species from about 90 trap-nights to ca. 650 trap-nights, with a third species added at that point, but none further added up to ca. 1000 trap-nights. There was no evidence of reaching plateaus at localities 1 (780 m), 3 (900 m), 4 (1040 m), and 5 (1300 m), indicating the capture of additional species might still be possible. We excluded *Suncus murinus* in this assessment of sampling adequacy because it is a non-native species and not part of the natural community.

Our accumulation curves indicate that our overall sampling effort may have been sufficient to obtain all the species of native nonvolant small mammals (6 species) on Mount Palali because a relatively long plateau of 2900 trap-nights was reached after reaching maximum species richness at 1400 trap-nights. Also, we obtained three or more individuals of each species. On the other hand, accumulation curves for individual localities suggest that sampling effort was not sufficient to document full species richness at most localities. A plateau was reached only at 1420 m (locality 7), after 700 trap-nights, which exceeded the number of trap-nights at all but one other locality (Fig. 3). As discussed below, this has implications regarding assessment of elevational patterns of species richness.

LARGE MAMMALS—Five species of large mammals were documented on Mount Palali, either by direct and indirect observations by us or through interviews with knowledgeable local hunters. Our trapping equipment was not appropriate to capture large mammals and thus we cannot provide estimates of abundance. We collected information only on the presence and absence and rough elevational extent of each large mammal species.

Elevational Patterns

FRUIT BATS—We recorded five species of small fruit bats; these were most diverse in the lowlands (localities 1 through 3) on Mount Palali (Table 1), with three or four species, whereas one or two species were recorded or inferred in montane and mossy forest. The decline in species richness with increasing elevation was statistically significant ($r_s = 0.95$, $P < 0.05$).

The proportional abundance of species across the five elevation localities showed significant variation (G-test; G = 403.71, d.f. 16, $P < 0.001$). *Ptenochirus jagori* was documented or inferred at all elevations except at the peak, whereas *Macroglossus minimus* was netted from lowland to transitional lowland–montane forest (locality 4). *Cynopterus brachyotis* and *Haplonycteris fischeri* occurred only in lowland forest, whereas *Otopteropus cartilagonodus* was captured only in mossy forest (1420 and 1707 m; Table 1). Comparisons of capture frequencies between lowland and mossy forest locality pairs (localities 1 and 3, and 7 and 8, respectively) showed significant bias for only one species because of small sample sizes. For the two most abundant species, we see strong but opposing effects of elevation: *C. brachyotis* was most abundant in lowland forest and lowland agroforest, whereas the restriction of *O. cartilagonodus* to the mossy forest locality pair was statistically significant (χ^2 = 206, $P < 0.001$). Locality pair comparisons for overall netting success showed significantly more captures in the mossy forest pair because of the abundance of *O. cartilagonodus* (46 individuals). Overall relative abundance of fruit bats was not correlated with elevation ($r_s = 0.35$, $P > 0.05$).

Insectivorous Bats—As stated earlier, our netting effort and captures were limited, so few generalizations are possible. We know of at least four species within the lowland localities (localities 1, 2, 3), whereas five and three species were inferred or captured in montane and mossy forests, respectively (Table 2). *Rhinolophus arcuatus* and *R. inops* were recorded or inferred at all elevations; *Hipposideros ater* was recorded in lowland to transitional lowland–montane forest; *Rhinolophus virgo* and *Kerivoula whiteheadi* were captured only in transitional lowland/montane forest at 1040 m; *Pipistrellus javanicus* was captured only in mossy forest at 1420 and 1707 m; and *H. diadema* was captured only in lowland forest at 900 m. *Rhinolophus arcuatus* and *P. javanicus* were most abundant in mossy forest, whereas *R. inops* was captured most often in lowland agroforest–dipterocarp forest (Table 2).

We captured a total of 70 microchiropterans with mist nets and V-nets. Although more individuals were captured using mist nets (45) compared with V-nets (25), total capture rate for V-nets was substantially higher than for mist nets (Table 2), but the different techniques (e.g., rates measured in hours for V-nets and net-nights for mist nets) make statistical testing inappropriate. V-nets captured more species (6) than did mist nets (4); three species, *H. ater*, *R. virgo*, and *K. whiteheadi*, were captured solely with V-nets, and one, *H. diadema*, was captured only with a mist net.

As noted above, these data should be taken only as rough indications of patterns, because our sampling of insectivorous bats was certainly incomplete.

Non-volant Small Mammals—We recorded a total of seven species of non-volant small mammals: two shrews (1 native and 1 nonnative) and five native murid rodents (Table 3). Species richness hardly varied across the elevational transect and was not statistically correlated with elevation ($r_s = 0.064$, $P > 0.05$); localities 1 and 3 (lowlands) both had four species; localities 4 and 6 (montane forest) had five species (captured and inferred); and localities 7 and 8 (mossy forest) had five and four species, respectively. Except for localities 7 and 8, sampling effort was less than 500 trap-nights in total (Table 2), and the species accumulation curves (Fig. 3) did not reach plateaus, both of which imply that actual species richness probably was not measured. This could have affected the species richness pattern we found on Mount Palali, and we therefore treat the pattern as provisional.

Total relative abundance (unweighted, measured as the number of small mammals captured per 100 trap-nights, standardized to equal numbers of earthworm and coconut baits; Table 3) was higher in both lowland (localities 1 and 3) and mossy (localities 7 and 8) forest localities than in montane forest (localities 4 and 6). The correlation between elevation and abundance that is often found (e.g., Rickart et al., 2011) is not statistically significant ($r_s = 0.037$, $P > 0.05$), which could be attributed at least in part to insufficient sampling.

Variation in the proportional abundances of native species among the six localities was significant (G-test; G = 218.2, d.f. 25, $P < 0.001$). *Crocidura grayi*, *Apomys sierrae*, *Chrotomys* sp. 1, and *Rattus everetti* either occurred (or were inferred) over the entire transect or were absent only in the lowest, most disturbed locality, except that *R. everetti* was absent at the uppermost locality. *Apomys microdon* occurred in montane and mossy forest at 1040 m and above, and *Chrotomys* sp. 2 was captured solely in lowland agroforest–dipterocarp forest (Table 3). Comparisons of capture frequencies at low-, middle-, and high-elevation pairs of localities (representing lowland agroforest and disturbed lowland forest, montane forest, and mossy forest habitat zones, respectively) showed significant elevational bias in one species. *Chrotomys* sp. 1 was significantly more abundant in both lowland (χ^2 = 36.53, $P < 0.001$) and mossy forest (χ^2 = 10.12, $P < 0.001$) than in montane forest. Although *Chrotomys* sp. 2 was captured only in lowland forest and *A. microdon* only in montane and mossy forest, their patterns were not statistically significant because of low numbers. *Apomys sierrae* was equally abundant in all three habitat types, with the number of captures directly proportional to the number of trap-nights at each locality (Table 3).

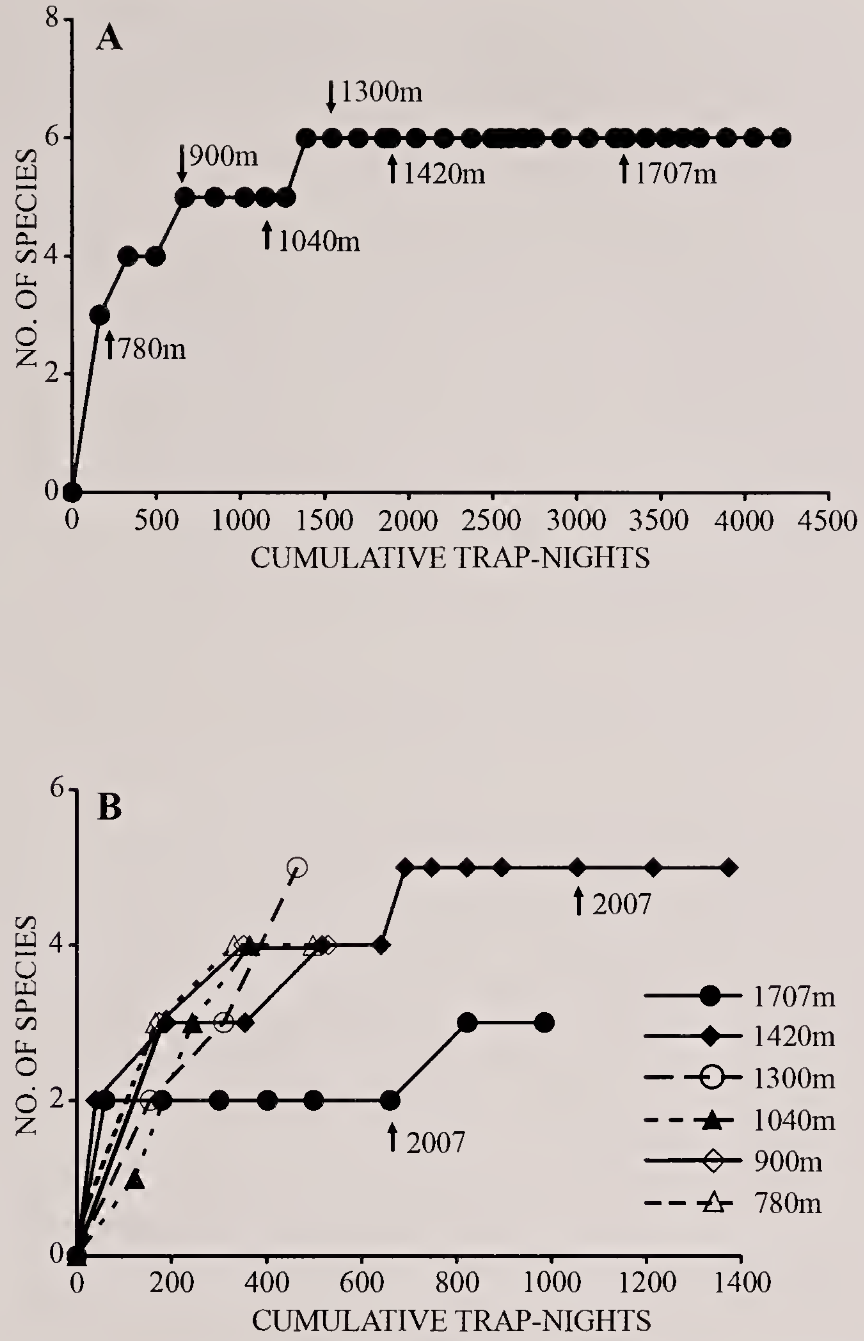

Fig. 3. Species accumulation curves for native non-volant small mammals on Mt. Palali in (**A**) all field surveys and (**B**) individual localities (see Study Area).

Capture data revealed that overall diel activity patterns of native species were, in the aggregate, significantly nocturnal/crepuscular (χ^2 = 155.12, $P < 0.0001$; Table 4). Within species, significant nocturnal/crepuscular activity patterns were seen in *A. sierrae* (χ^2 = 116.92, $P < 0.0001$), *A. microdon*

TABLE 4. Number of captures by bait type and diel period for native non-volant small mammals on Mt. Palali. Trap-nights (calculated from the elevations where the species occurred; see Materials and Methods) are shown in brackets and captures per 100 trap-nights in parentheses. Captures greater than expected (on the basis of χ^2 tests, except where noted) are designated by boldface. Overall trap success is the sum of trap success for individual species.

Species	Bait type		Diel period	
	Coconut	Worm	Nocturnal/Crepuscular	Diurnal
Crocidura grayi	3 [2041] (0.15)	3 [1156] (0.26)	3	3
Apomys sierrae	112 [2504] (4.47)	71 [1547] (4.59)	**179**[a]	4
Apomys microdon	**7**[b,c] [2201] (0.32)	0 [1064] 0	**7**[b,c]	0
Chrotomys sp. 1	22 [2504] (0.88)	**27**[b] [1547] (1.74)	**45**[a]	4
Chrotomys sp. 2	1 [250] (0.40)	3 [239] (1.26)	4	0
Rattus everetti	**12**[b] [1981] (0.61)	3 [1164] (0.26)	**15**[a]	0
Total captures	157	**107**[a]	**253**[a]	11
Overall trap success (per 100 trap-nights)	6.83	8.11	6.25	0.27

[a] $P < 0.01$.

[b] $P < 0.05$.

[c] Significance tested with binomial distribution.

(binomial distribution, $P < 0.04$), *Chrotomys* sp. 1 ($\chi^2 = 25.13$, $P < 0.0001$), and *R. everetti* ($\chi^2 = 10.86$, $P < 0.0001$); all four individuals of *Chrotomys* sp. 2 were captured during nighttime as well, but this was not statistically significant. *Crocidura grayi* showed no significant diel pattern ($\chi^2 = 0.46$, $P > 0.05$); although the sample size is low, this clearly indicates activity during both day and night. Among rodents, *A. sierrae* and *Chrotomys* sp. 1 captures included ca. 2% and 8% diurnal captures, respectively.

Native species differed in their responses to the two baits used with ground traps (Table 4). Earthworms were significantly more effective in attracting *Chrotomys* sp. 1 ($\chi^2 = 4.72$, $P < 0.05$), whereas coconut was more effective for *A. microdon* ($\chi^2 = 5.21$, $P < 0.05$) and *R. everetti* ($\chi^2 = 4.93$, $P < 0.05$). Bait attractiveness was not significantly different for *A. sierrae*, and samples for *C. grayi* and *Chrotomys* sp. 2 were too small to test. Trap success for each bait type differed markedly with varying elevations as well. Correlation between elevation and trap success with coconut bait was significantly negative ($r_s = 0.74$, $P < 0.05$), implying that small mammal use of seed-like foods declined with increasing elevation. Overall trap success with earthworm bait was highest at the mossy forest localities, but the correlation was not statistically significant. For *R. everetti*, the negative correlation between elevation and trap success with coconut bait was significant ($r_s = 0.71$, $P < 0.05$).

Apart from the six species of native small mammals, we captured two individuals of the non-native shrew *S. murinus* in the grassland adjacent to the forest-line at the 675-m elevation locality. This species was not captured elsewhere on the mountain, even in regenerating forest habitat in the lowlands or in *kaingin* farms surrounded by forest habitat. On the other hand, five native species (*C. grayi, A. sierrae*, *Chrotomys* sp. 1 and 2, and *R. everetti*) were trapped in grassland adjacent to forest and *kaingin* farms. We captured only native species in forested habitats on Mount Palali. No non-native rats (e.g., *Rattus exulans* or *Rattus tanezumi*) were captured at any locality during this study.

LARGE MAMMALS—We obtained direct evidence and reliable reports for five large mammals on Mount Palali. One of these, the Philippine warty pig (*Sus philippensis*), was described by local hunters as abundant at all elevations, including nearby agricultural fields and swiddens (*kaingin*). We encountered pig wallows at almost all elevations as well. This large mammal was frequently hunted, usually with snares, shotguns, or makeshift explosive balls. Hunting usually commences during August to coincide with the fruiting of *manaring* (oaks, *Lithocarpus* spp.), and ends in late January. We encountered fecal signs of two species of civets, *Paradoxurus hermaphroditus* and *Viverra tangalunga*, across all elevations except at the peak, and our guides reported that they were hunted with the use of dogs to flush them out. We observed the long-tailed macaque (*Macaca fascicularis*) at the 1300-m locality. Our guides reported that this monkey is frequently seen in *kaingins* and in banana orchards and cornfields in the lowlands. The northern Luzon giant cloud rat (*P. pallidus*) was documented by reports from hunters. They seldom hunt this large murid and captures were mostly not purposive, usually taking place when hunting wild pigs. Hunters observed cloud rats in lowland forest with tall dipterocarps. We did not encounter the Philippine brown deer (*Cervus mariannus*), said by hunters to have been absent on Mount Palali since the early 1990s and to have been hunted heavily before that time.

Discussion

Fruit Bats

Among the five species of fruit bats captured, *Haplonycteris fischeri* and *Ptenochirus jagori* are widespread Philippine endemics, and *Otopteropus cartilagonodus* is restricted to Luzon Island, whereas *Cynopterus brachyotis* and *Macroglossus minimus* are widespread across Southeast Asia. Our netting data (although limited) indicate that fruit bat species richness on Mount Palali was highest in the lowlands and declined significantly with increasing elevation. This pattern is seen also on Mount Isarog in southeastern Luzon, Mount Guinsayawan on Negros, Mount Pangasugan on Leyte, Mount Timpoong on Camiguin, and Mount Kitanglad on Mindanao (Rickart et al., 1993; Heaney et al., 1989, 1998, 2006a,b).

The reason for the decline in species richness is unclear, although Heaney et al. (1989) suggested that environmental and habitat changes associated with mossy forest may play a predominant role, such as cold temperature and reduction in abundance of *Ficus* (Heideman & Heaney, 1989). Utzurrum (1984) reported that *C. brachyotis*, *H. fischeri*, and *P. jagori* rely heavily on fruits of *Ficus* throughout much of the year. Our results on Mount Palali are consistent with Heaney et al. (1989) on the factors contributing to the decline, in that we observed that mossy forest, particularly near the peak, was devoid of *Ficus* and temperature was much lower than at lower elevations. Our netting data also showed the fruit bat community composition to be different at the low and high elevations: *C. brachyotis*, *H. fischeri*, and *M. minimus* were recorded mainly at low elevations, whereas *O. cartilagonodus* was captured solely at high elevations. This pattern is consistent with surveys in other parts of Luzon, wherein *C. brachyotis* and *M. minimus* are generally more common in disturbed lowland habitats, *H. fischeri* is typically more common in primary lowland forest, and *O. cartilagonodus* is generally more abundant at high elevations (Heaney et al., 1989, 1999, 2003).

Heaney et al. (1998) reported *D. leucopterus* and *P. hypomelanus* to be present within the broad vicinity of Mount Palali. Together with our survey results, this brings the total number of fruit bats known for the Caraballos to seven species. Nonetheless, we consider our netting effort to be insufficient because we failed to document at least five species of small fruit bats (*E. spelaea* and *E. robusta*, *D. rickarti*, *H. whiteheadi*, and *R. amplexicaudatus*) known from Luzon, two of which (*E. spelaea* and *R. amplexicaudatus*) are common and widespread.

Insectivorous Bats

No detailed estimates of Philippine microchiropteran faunal richness across an elevational transect are available, and few comparisons are possible. With seven species documented, Mount Palali compares poorly with the 15 species recorded from Catanduanes (Heaney et al., 1991), the 17 from Leyte (Rickart et al., 1993), 17 from Mount Kitanglad, Mindanao Island (Heaney et al., 2006b), 22 from Mount Makiling, Laguna Province (Sedlock, 2002), and 23 from Mt. Banahaw (Sedlock et al., this volume).

We believe our tally of seven species of insectivorous bats on Mt. Palali to be quite incomplete and not usable for estimating species richness and community composition patterns. We know from our capture data that at least four species are present in lowland forest and lowland agroforest, five in montane forest, and three in mossy forest. Heaney et al. (1998) reported two additional species (*Taphozous melanopogon* and *Myotis rufopictus*) within the provinces of Nueva Ecija, Nueva Vizcaya, and Quirino, where the Caraballo Mountains lie. Together with our survey results, this means that at least nine species of insectivorous bats are present within the Caraballo Mountains.

It should be noted that our V-netting effort, although limited, captured six of the seven total species (including 3 species that were captured solely by V-nets). Similarly, Duya et al. (2007) captured 11 of the total 15 insectivorous bats in a mammal survey of the Sierra Madres, Luzon Island, using V-nets. We believe that surveys of insectivorous bats must entail a wide variety of capture methods (in addition to mist nets and V-nets), such as harp traps and tunnel traps (Sedlock, 2001, 2002; Sedlock et al., this volume) and subcanopy mist nets (Ingle, 1993), to fully document insectivorous bat diversity.

Non-volant Small Mammals

Of the seven non-volant small mammals we recorded from Mount Palali, *Suncus murinus* is a non-native species, *Rattus everetti* is a widespread Philippine endemic, *Crocidura grayi* occurs on Luzon and Mindoro Island, *Apomys microdon* is confined to Luzon and Catanduanes islands, and *A. sierrae* is a recently described species shared by Mt. Palali with the northern Sierra Madre (Heaney et al., this volume). Of the two clearly distinct species of *Chrotomys* present on Mount Palali, one or both could prove to be undescribed species (E. A. Rickart, unpubl. data). With taxonomic examinations still underway, we cannot determine whether Mount Palali or the Caraballo Mountains harbor locally endemic species and represent a distinctive subcenter of mammalian endemism within Luzon Island similar to the Central Cordillera, Mount Isarog, the northern Sierra Madre, and the Zambales Mountains (Heaney et al., 1999, 2003, this volume; Ong et al., 2002; Balete et al., 2009).

On our elevational transect, we observed little variation in species richness of native non-volant small mammals, with four at the lowest elevations (localities 1 and 3), five at middle elevation (localities 4, 6, and 7), and four at the peak (locality 8). Overall unweighted relative abundances per locality on Mount Palali were not statistically correlated with elevation: the values for the lowest and highest localities were higher than those for middle elevations. Species composition did not vary greatly across the elevational transect; only two species differed between the major habitat types. *Chrotomys* sp. 2 occurred only in the lowlands, whereas *A. microdon* was trapped only in montane and mossy forest; the remaining four species (*C. grayi*, *A. sierrae*, *Chrotomys* sp. 1, and *R. everetti*) were present in all major habitat types. Other Philippine mountains exhibit increasing species richness and relative abundance with elevation and the presence of a distinct community of non-volant small mammals in mossy forest, as documented in the Central Cordillera, Mount Isarog, Mount Kitanglad, Mount Tapulao in the Zambales Mountains, and the Mingan Mountains (Rickart et al., 1991, 2011; Heaney et al., 1999, 2003, 2006b; Heaney, 2001; Balete et al., 2009, this volume). The trend we documented on Mt. Palali appears to be inconsistent with these patterns. Nevertheless, our sampling effort at most of the localities was not exhaustive (localities 1, 3, 4, and 6) so that the maximum species richness and accurate measurement of relative abundance probably were not achieved for these localities.

On the basis of our trapping data, bait attractiveness and diel activity pattern varied among the six native species. *Apomys microdon* and *R. everetti* were nocturnal and strongly attracted to coconut baits; *Chrotomys* sp. 1 and 2 were generally nocturnal and favored earthworms (although some daytime captures and attraction to coconut bait were also documented); *Crocidura grayi* was attracted indiscriminately to both bait types and was active during day and night; *A. sierrae* also was attracted to both baits but was significantly more active at night. Our results generally agree with those reported for related species on other mountains on Luzon (Heaney et al., 1989, 1999; Rickart et al., 1991, 2011; Balete et al., 2009), although *C. grayi* favored earthworms more on Mount Isarog and in the Zambales Mountains, and *Chrotomys mindorensis* in the Zambales Mountains was more active during daytime than its Mt. Palali congeners. Our results showed that trap success with coconut baits decreased significantly with elevation, whereas attractiveness of earthworm bait was highest in mossy forest. These data are consistent with those reported by Rickart et al. (1991) and Balete et al. (2009) on Mount Isarog and Mount Tapulao in the Zambales Mountains, respectively, which showed a dietary shift with increasing elevation from granivory/omnivory to an increasing percentage of omnivory/vermivory. Although we had only 11 daytime captures, 10 of them occurred in mossy forest (localities 7 and 8). This could suggest that diurnal activity is most prevalent at higher elevations on Mount Palali, as was the case on Mount Isarog and Mount Tapulao (Rickart et al., 1991; Balete et al., 2009).

With the exceptions of *A. microdon,* which was present only in undisturbed forest, and *Chrotomys* sp. 2, which was present only in disturbed forest, all native species were caught in both undisturbed forest and newly regenerating lowland second-growth forest (a remnant of past logging activities), and some also were taken in grassy second-growth and old *kaingin* farms at forest edges. This demonstrates that most of the native small mammals can tolerate at least some habitat disturbance. The non-native *S. murinus,* on the other hand, was captured only in anthropogenic grassland near forest and not in the forest interior, nor in newly regenerating lowland second-growth forest. We did not capture other non-native common pest species such as *Rattus exulans* and *R. tanezumi.* Our results suggest that native species on Mount Palali have maintained their presence despite the occurrence of various habitat disturbances at the forest edge and interior and do not show any evidence of being displaced by non-native species. The inability of non-native species to penetrate either primary or disturbed but regenerating forest habitats has been observed elsewhere in the Philippines: on Mount Isarog, the Mount Bali-it area of the Central Cordillera, and Mount Tapulao in the Zambales Mountains (Rickart et al., 1991, 2011; Heaney et al., 1999, 2003; Balete et al., 2009). Heaney et al. (1999) hypothesized that resistance to invasion is, in part, a function of native diversity and that on oceanic islands, the success of invasion by non-native small mammals is determined by the number of species in the community of native small mammals. It should be noted that Mount Bali-it, Mount Tapulao, and Mount Isarog have 12, 9, and 8 native species, respectively. Three non-native species (*S. murinus*, *R. exulans*, and *R. tanezumi*) have been found to be abundant in forest on Negros (2 native small mammals) and moderately common in forest on Camiguin (5 native small mammals; Heaney et al., 1989, 2006a). The results of our Mount Palali survey, despite the relatively low number of native species present (7 including *Phloeomys pallidus*) compared with other Philippine mountains, clearly are consistent with this hypothesis.

A striking result of our survey of non-volant small mammals on Mount Palali is the apparent absence of some genera of murid rodents. Despite an effort of nearly 4300 trap-nights, we did not capture four genera of murid rodents (*Archboldomys*, *Batomys*, *Bullimus*, and *Rhynchomys*) that are readily captured in mossy forest in some other parts of Luzon (Rickart et al., 1991, 2011; Heaney et al., 1999, 2003; Duya et al., 2007; Balete et al., 2009). Previous studies of small mammals along elevation gradients in the Philippines have documented a consistent pattern of maximum species richness on mountains reaching elevations near or exceeding 2000 m. On Luzon Island, Mount Bali-it, in the Central Cordillera (peak = 2250 m), has 13 native species (Heaney et al., 2003; Rickart et al., 2011); Mount Isarog (1966 m) has eight native species (Rickart et al., 1991; Heaney et al., 1999); and Mount Tapulao (2037 m) has nine native species (Balete et al., 2009). These mountains have all or most of the four murid rodent genera that we did not capture on Mount Palali. Our species richness tally of six native non-volant mammals on Mount Palali (which peaks at 1707 m) appears to be consistent with this general pattern of maximum species richness threshold. No mountains within the Caraballos are higher than about 1700 m, much less 2000 m, so it is likely that some genera, particularly *Batomys* and *Rhynchomys*, might be entirely absent from the mountain range. On the other hand, *Archboldomys* and *Bullimus* have been recorded at lower elevations in the Sierra Madre (Duya et al., 2007, this volume). *Archboldomys musseri* is known to be present at 1650 m on Mount Cetaceo in the northern Sierra Madre (Rickart et al., 1998), whereas *Bullimus* occurs from lowland forest to mossy forest (Duya et al., 2007, this volume). There are other forested peaks within the Caraballos, particularly Mount Mamparang (ca. 1450 m), on which *Archboldomys* and *Bullimus* may occur. Trapping on this mountain could test the absence of these murid genera from the Caraballos.

Large Mammals

Our records of the five large mammals on Mount Palali indicate that almost all are present across the elevational transect, from lowland agroforest and lowland dipterocarp forest through montane forest to mossy forest. We are not certain whether *Phloeomys pallidus* is present at higher elevations on Mount Palali, although our local guides thought that it might be. Elsewhere on Luzon Island, Heaney et al. (1998) reported this murid from sea level to at least 2000 m. Hunters singled out *Sus philippensis* as being abundant at all elevations, even in lowland agroforest; we agree with this because we encountered high numbers of distinctive signs (e.g., pig wallows) at all elevations.

Local guides also reported that virtually all large mammals on Mount Palali are still being hunted, mainly for local consumption. We did not encounter any Philippine brown deer during our survey, and local hunters had not encountered this animal on the mountain for at least 15 years. Deer were heavily hunted before their disappearance.

Conclusion and Recommendations

A total of 24 species of mammals was recorded along the elevational transect on Mount Palali. This total comprises two shrews (1 native and 1 non-native), five fruit bats, seven insectivorous bats, one macaque, six native murid rodents, two civets, and one pig. On the basis of museum records, an additional five species (2 large fruit bats, 2 insectivorous bats, and 1 alien pest rat) also are present within the municipalities near Mount Palali, and they probably are present within the Caraballo Mountains. Our elevational transect found several different diversity patterns in different mammal groups: bats were most diverse at low elevation, non-volant small mammals showed no significant variation in species richness along the elevation gradient (although some species were elevationally restricted), and most species of large mammals were present at all elevations.

We captured or recorded 18 native species (78% of the total native species) within the lowland forest. This lowland forest, particularly below 900 m, is highly degraded because of previous logging operations and the continuing practice of slash-and-burn farming. This contrasts with the high-elevation forest, in which anthropogenic disturbances have been minimal. Additionally, interviews with our local guides indicated that much of the hunting of large mammals occurs in the lowlands. This highlights the lowland forest of Mount Palali as an important but imperiled habitat and supports creation of a protected area (or its equivalent tenurial instrument) that includes this habitat, as well as the mature forest at higher elevations.

Our results show that many of the native species appear to be able to tolerate at least some habitat disturbance, whereas non-native pest species were not captured (and probably are not present) in forested habitats, even in newly regenerating lowland forest. It is important that these marginal habitats be protected and designated as a restoration zone to insure the commencement of forest regeneration and further minimize the invasion of non-native and invasive pest mammals.

We recorded 14 native species in the high-elevation mossy forest, with five species solely in that habitat. We believe that for the whole mammalian biodiversity of Mount Palali to be protected in perpetuity, all habitat types, from disturbed and regenerating lowland forest to high-elevation forest, must be included in any protection program. Such a protected area would be most effective if it were a single, contiguous area. Furthermore, we note that Mt. Palali and the Caraballo Mountains could serve as part of a corridor of natural habitat that would connect the Central Cordillera to the Sierra Madre, thus contributing to the stability of wildlife and watersheds throughout much of Luzon (Ong et al., 2002; Catibog-Sinha & Heaney, 2006).

The forest of Mount Palali serves as one of the major watersheds in the Caraballo Mountains that act as the headwaters of many major rivers providing water to the provinces of Nueva Ecija, Nueva Vizcaya, and Quirino. Protection of the forest on Mount Palali (and the rest of the Caraballo Mountains) will not only help sustain the remarkable mammal fauna but also serve the interests of the people of Central Luzon, who require protection from flooding and drought and access to clean, abundant water. The efforts of local conservation groups, particularly Friends for the Environment for Development and Sustainability, Conservation International–Philippines (CI-P), and the Philippine Department of the Environment and Natural Resources (DENR) deserve commendation for recognizing the biological importance of Mount Palali and the Caraballo Mountains. They have now established a project that will facilitate the declaration of a sizable portion of the Caraballo Mountains (including Mount Palali) as a protected area.

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Chapter 3: The Mammals of the Mingan Mountains, Luzon Evidence for a New Center of Mammalian Endemism

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Abstract

We conducted an elevational transect survey of mammals on the highest peak in the Mingan Mountains of Aurora and Nueva Ecija provinces in the central Sierra Madre Range of Luzon from May to August 2006 and documented 35 species of mammals. These included one shrew (Soricidae), six fruit bats (Pteropodidae), one ghost bat (Megadermatidae), three horseshoe bats (Rhinolophidae), three roundleaf bats (Hipposideridae), four evening bats (Vespertilionidae), one macaque (Cercopithecidae), 12 mice and rats (Muridae), two civets (Viverridae), one wild pig (Suidae), and one deer (Cervidae). Our survey of this small, poorly known mountain range included the discovery of two new species of forest mice (*Apomys*), a new species of shrew-mouse (*Archboldomys*), a probable new species of shrew-rat (*Rhynchomys*), and an unidentified species of tube-nosed bat (*Murina*). Species richness of bats decreased with increasing elevation, whereas that for native non-volant small mammals increased with increasing elevation up to 1677 m, then declined at 1681 and 1785 m. Statistically significant diel activity and bait preferences were observed among the native non-volant small mammals. Only the two species of small forest mice (*Apomys microdon* and *A. musculus*) were captured exclusively above ground; the other non-volant small mammals were nearly always captured on the ground. The Mingan Mountains, with either three or four endemic species, are clearly a significant center of mammalian endemism, deserving of conservation.

Introduction

The Sierra Madre Range is often described as the longest mountain range in the Philippines, hugging the eastern coast along the Pacific Ocean from the northeast tip of Luzon in Cagayan Province to the area east of Manila and Laguna de Bay in Quezon Province. It has been recognized as one of the priority conservation areas in the Philippines and currently has the largest contiguous and relatively intact representation of tropical forest habitats, and the largest national park, on Luzon (Mallari et al., 2001; Ong et al., 2002).

However, rather than being a single, continuous mountain chain, the Sierra Madre Range consists of three separate geological and topographic units along its length (see fig. 3 in Heaney et al., this volume). The northernmost and longest of these units, making up about two-thirds of the entire length of the Sierra Madre, extends from San Vicente in Cagayan Province south to Baler in Aurora Province. The southernmost section, about a third the length of the northernmost, extends from Dingalan in Aurora Province at its northern edge to its southernmost end in Atimonan, Quezon Province. Although the middle section, the Mingan Mountains, has one of the highest peaks in the entire Sierra Madre at 1901 m elevation, it is the smallest of the three units. It is a compressed triangular landmass wedged between the two larger units, separated from them at the northern and southern boundaries by narrow but deep lowland valleys drained by rivers that run to the Philippine Sea (a part of the Pacific Ocean), and from the Caraballo Mountains on the west by the tributaries of the Cagayan River and Pampanga River. Each of the three units is geologically complex and unique, as revealed by its stratigraphy and distinctive geological history (Bureau of Mines and Geo-Sciences, 1981; Hashimoto, 1981). The significance of this area to the biogeography of Luzon, in particular, and to the Philippines in general, is still poorly understood (Heaney, 1986).

Until recently, knowledge of the mammalian diversity of the Sierra Madre was poor and fragmentary. The northern Luzon shrew-mouse, *Crunomys fallax*, was the only endemic non-volant mammal known from the Sierra Madre prior to the 1990s and is still known from only a single specimen from the lowlands of Isabela Province, taken in the 1890s (Thomas, 1898; Musser, 1982; Musser & Heaney, 1992; Rickart et al., 1998). In the 1980s, the first records of bats were produced by a survey of the lowland forest in Maconacon, on the eastern coast of Isabela Province (Mudar & Allen, 1986), followed in the 1990s by the first extensive records for vertebrates (Danielsen et al., 1994), including the description of the Sierra Madre shrew-mouse, *Archboldomys musseri*, from Mt. Cetaceo (Rickart et al., 1998). In the early 2000s, a series of preliminary surveys of mammals was conducted on several peaks of the Sierra Madre, mainly concentrated in the northern portion of the range (8 sites in Cagayan and 2 in Quirino provinces), but also in one locality in the southern section (Quezon Province), resulting in the first general summary of the mammals of the Sierra Madre (Duya et al., 2007) and the description of a forest mouse (*Apomys sierrae*) endemic to the northern Sierra Madre and the Caraballo Mountains (Heaney et al., this volume).

The above-mentioned surveys indicate a center of mammalian endemism in the northern section of the Sierra Madre, with the presence of *Crunomys fallax* and *Archboldomys musseri*, both found nowhere else (Rickart et al., 1998), and *Apomys sierrae*, shared by the northern Sierra Madre and the Caraballo Mountains (Heaney et al., this volume). Similar surveys in other parts of Luzon resulted in the identification of several other centers of endemism, including the Central Cordillera, the Bicol Peninsula, and the Zambales Mountains (Heaney et al., 1998; Heaney & Regalado, 1998; Ong et al., 2002; Heaney, 2004; Balete et al., 2006, 2007, 2009; Alviola et al., this volume; Duya et al., this volume; Rickart et al., 2011). Until the time of the survey reported here, the mammals of the central unit of the Sierra Madre were unknown, and those of the southern unit remain nearly unknown at this time. This survey was designed to address the gap in our knowledge of the small mammals of the Mingan Mountains, with the expectation that previously unknown species might be found and that previously poorly known species would be further documented. Specifically, we sought to conduct a thorough survey of small mammals along the elevational gradient to determine patterns of species richness and relative abundance, assess the taxonomic status of each species, and document basic ecological features of each species, including arboreal vs. ground-surface activity patterns, diurnal vs. nocturnal activity, attractiveness of "seed" and "animal" bait, and general habitat association. We also collected data on bats and large mammals (civets, cloud rats, deer, macaques, and wild pigs) on a less intensive basis.

In this paper we present the results of our survey of the Mingan Mountains in 2006, detailing the ecology of 35 species of bats and nonvolant mammals, including two new species of forest mice (*Apomys aurorae* and *A. minganensis*; Heaney et al., this volume), a new species of shrew-mouse (*Archboldomys*; D. S. Balete, unpubl. data), and others still under study, including the first record of a shrew-rat (*Rhynchomys*) anywhere in the Sierra Madre, a striped earth-mouse (*Chrotomys*), and a small tube-nosed bat (*Murina*).

Methods

Study Localities

Our survey of mammals in the Mingan Mountains was conducted principally on the slopes of the highest peak, Mt. Mingan (maximum elevation 1901 m), from 27 May to 26 June 2006; in habitats ranging from lowland dipterocarp forest at ca. 559 m to mossy forest at 1785 m; and on 12–13 August 2006 in a reforestation site surrounded by agricultural lands at ca. 100 m (Fig. 1). The May–June study was undertaken at localities on the southwestern and southeastern slopes of Mt. Mingan along a trail on top of a ridge leading up to ca. 1800 m. The trail was said to be used mainly by members of the Dumagat ethnic group from the west side of the Mingan Mountains to access Dumagat settlements near the east coast and vice-versa, as well as by lowland farmers, all of whom hunt for wildlife and gather rattan and other forest products in the surrounding forest.

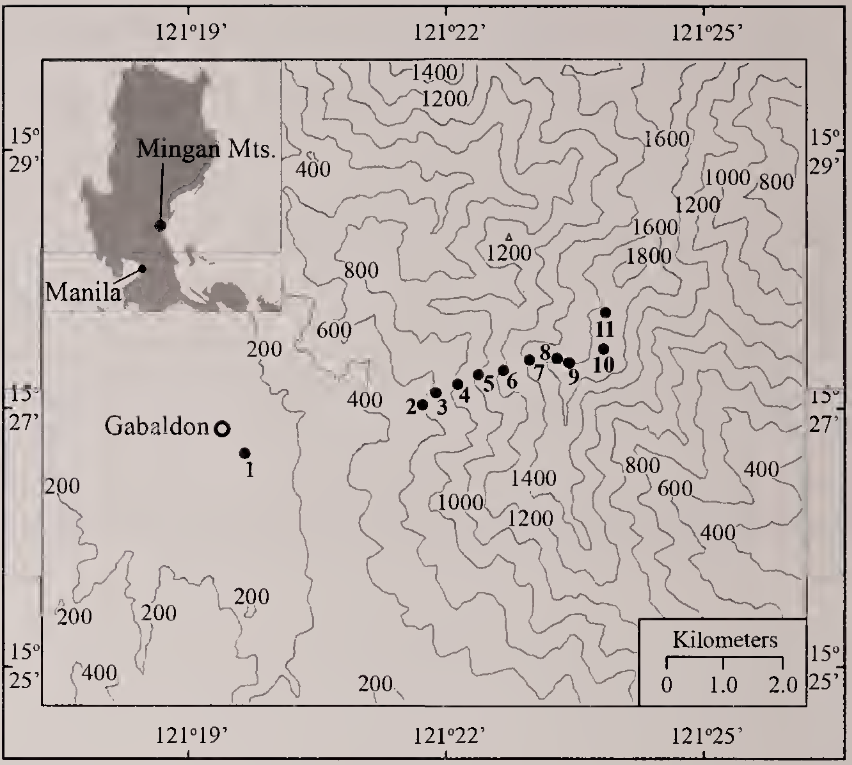

FIG. 1. Map of the Mt. Mingan study area, with sampling localities indicated by **solid circles** and numbered as in the list of localities (see Methods). Contour intervals equal 200 m. Inset shows the location of Mt. Mingan on Luzon Island.

The trail followed a ridge on the southwest slope of Mt. Mingan to ca. 1500 m. Our survey localities from ca. 559 to 1305 m were located along the top and on both sides of this ridge. Then the trail turned eastward, leading to the southwest slope's highest point, and connecting to the southeast slope of the mountain at ca. 1600 m. Survey localities at 1476 and 1540 m were on the southeast and north sides, respectively, of this ridge, whereas our 1677 m locality extended to the north and south of this ridge.

The trail appeared to have been unused recently above 1600 m. We re-established an overgrown trail that began at 1600 m to extend access toward the peak, following a steep, north-trending ridge, but reached only ca. 1800 m because of the difficulty of cutting through the thick stand of *Freycinetia* tangled with climbing bamboo and erect *Pandanus*. Our last two localities, at 1681 and 1785 m, covered mainly the flatter upper side to the west of this ridge.

The survey localities are described below from lowest to highest elevation (see Fig. 1):

LOCALITY 1—3.5 km S, 6.7 km W Mt. Mingan peak, 100 m elev., 15.45125°N, 121.34238°E (12–13 August 2006). This locality was situated on the campus of the Nueva Ecija University of Science and Technology, Gabaldon Municipality, Nueva Ecija Province. Ground-trapping for nonvolant mammals and mist netting for bats were conducted in a reforestation area planted with non-native mahogany (*Swietenia macrophylla*) and coffee (*Coffea* sp.). The undergrowth consisted largely of weedy shrubs and herbs. We had a total of 10 net-nights and 198 trap-nights at this locality.

LOCALITY 2—2.6 km S, 3.5 km W Mt. Mingan peak, 559 m elev., 15.45902°N, 121.37114°E (22–24 June 2006). The lowland dipterocarp forest at this locality (Fig. 2C) was relatively intact. The canopy, including emergents, was ca.

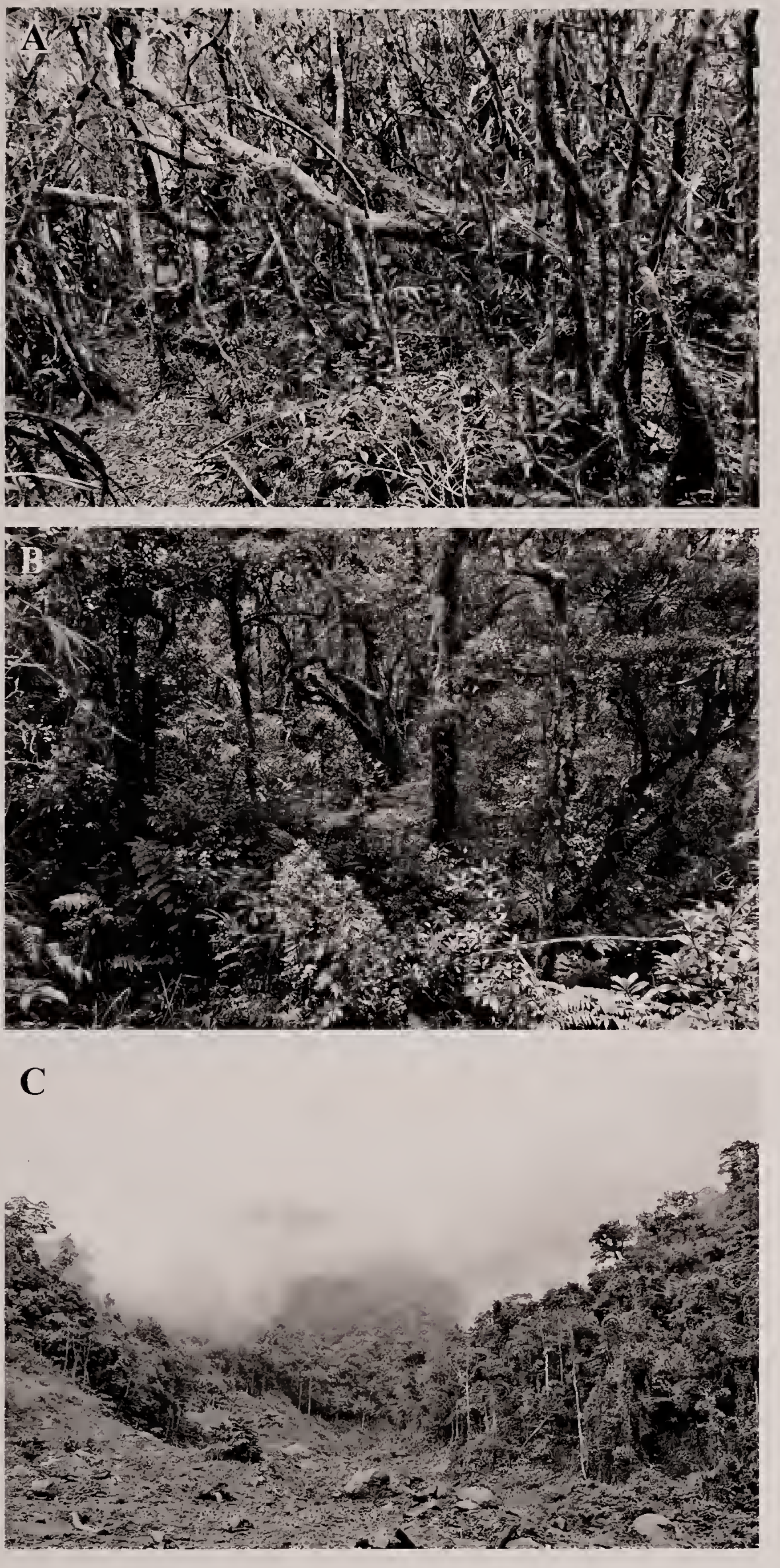

FIG. 2. Representative habitats on Mt. Mingan, showing: (**A**) mossy forest at 1677 m. In foreground, note climbing bamboo (*Schizostachyum*), climbing pandan (*Freycinetia*), and rattans (*Calamus*). June 2006, M. R. M. Duya. (**B**) Montane forest at 1305 m. Note in foreground climbing bamboo (*Schizostachyum*) and forest floor vegetation, including ferns and saplings. June 2006, M. R. M. Duya. (**C**) Lowland dipterocarp forest at 559 m (left and right sides) and 733 m (center left), viewed from an eroded riverbank, at ca. 400 m. June 2006, D. S. Balete.

35–45 m high, with the dominant species belonging to *Shorea* and other Dipterocarpaceae. Other canopy taxa included *Dillenia*, *Diospyros*, *Elaeocarpus*, *Ficus*, *Pometia*, and *Xanthophyllum*. Understory or subcanopy vegetation comprised shorter trees, including smaller trees of the canopy species and representatives of *Canarium*, *Mallotus*, *Nauclea*, *Syzygium*, *Litsea*, and *Cinnamomum*. Common canopy vines included lianas (*Tetrastigma*, *Strongylodon*, and members of Annonaceae and Leguminosae) as well as rattans (*Calamus*) and, less commonly, climbing bamboo (*Schizostachyum*). Epiphytic ferns and orchids were common, especially on the understory trees. Strangler figs (*Ficus*), climbing pandan (*Freycinetia*), and *Philodendron* were also commonly observed attached to tree trunks and branches. Herbaceous plants including aroids, begonias, gingers (*Zingiber*), and ferns, as well as saplings of canopy trees and rattans (*Calamus* and *Daemonorops*), were common on the ground. We had a total of seven net-nights, two harp-trap-nights, and 447 trap-nights at this locality.

LOCALITY 3—2.25 km S, 3.25 km W Mt. Mingan peak, 733 m elev., 15.46092°N, 121.37325°E (22–24 June 2006). This locality was similar to locality 2 in habitat type and vegetation composition but was on a rather steep slope (Fig. 2C). We had a total of four net-nights, two harp-trap-nights, and 417 trap-nights at this locality

LOCALITY 4—2.1 km S, 2.9 km W Mt. Mingan peak, 902 m elev., 15.46233°N, 121.37679°E (19–21 June 2006). The forest at this locality was dominated by dipterocarps, but almost entirely by a single species (*Shorea polysperma*), along with myrtles (mainly *Syzygium*, with a sprinkling of *Tristaniopsis*), oaks (*Lithocarpus*), laurels (Lauraceae), and *Elaeocarpus*. This species composition suggests the beginning of a transitional lowland dipterocarp/montane forest. The canopy, including emergents, was lower (20–30 m) than that in the dipterocarp forest at 500–700 m, and lacked a distinct lower subcanopy. The epiphyte and canopy vine compositions were similar to those of the lowland dipterocarp forest, but with more abundant ferns, mosses, climbing pandan, and climbing bamboo along the trail. Ground vegetation was also similar to that of the lower elevation study areas, but was more abundant, including tall, erect pandans (*Pandanus*). We had a total of six net-nights, three harp-trap-nights, and 437 trap-nights at this locality.

LOCALITY 5—1.9 km S, 2.5 km W Mt. Mingan peak, 1074 m elev., 15.46393°N, 121.38015°E (19–21 June 2006). As at locality 4, the forest here appeared to be of the transitional lowland dipterocarp/montane type, but with marked reduction of the canopy height (ca. 15–20 m), particularly on top of and at the upper edges of the ridge traversed by the trail. The presence of montane forest elements such as *Lithocarpus*, *Syzygium*, and *Tristaniopsis*, along with the appearance of species such as *Leptospermum* (Myrtaceae), was more conspicuous here than at 902 m. Additional montane taxa such as *Podocarpus* and some members of Theaceae were present. Canopy vines were less common and smaller here than at locality 4, but epiphytic ferns and orchids, as well as mosses, were more abundant. Climbing pandans, erect pandans (*Pandanus*), *Pinanga* palms, and climbing bamboo were common along the trail. We had a total of six net-nights, three harp-trap-nights, and 402 trap-nights at this locality.

LOCALITY 6—2 km S, 2 km W Mt. Mingan peak, 1305 m elev., 15.46456°N, 121.38421°E (14–17 June 2006). The vegetation at this locality was characteristic of primary montane forest (Fig. 2B), but of markedly lower canopy, ca. 7–10 m, including emergents, because of its location on top of a ridge and consequent exposure to high winds. Canopy trees were primarily myrtles (Myrtaceae), the most conspicuous of which was *Tristaniopsis*, along with *Syzygium* and *Leptospermum*. Other abundant montane taxa included *Podocarpus*, *Lithocarpus*, *Vaccinium*, and members of Theaceae (*Ternstroemia*, *Cleyera*). Large canopy vines were rarer here, but smaller vines such as *Smilax* remained common. Climbing bamboo and climbing pandan were common, especially along the trail. Ferns, orchids, and mosses were common epiphytes. Ground ferns were common along the trail and an exposed section of the ridge; orchids, aroids, and gingers (*Zangiber*) were present in undisturbed areas of the forest. We had a total of 12 net-nights, six harp-trap-nights, and 707 trap-nights at this locality.

Locality 7—1.8 km S, 1.6 km W Mt. Mingan peak, 1476 m elev., 15.46620°N, 121.38846°E (10–13 June 2006). This locality was in primary lower montane forest very similar in structure to that of locality 6, but on a more sheltered southeast slope. Composition of canopy trees also was similar to that of locality 6, but marked by the reduction of *Tristaniopsis* and the prevalence of *Syzygium*. We had a total of 12 net-nights and 772 trap-nights at this locality.

Locality 8—1.7 km S, 1.3 km W Mt. Mingan peak, 1540 m elev., 15.46641°N, 121.39304°E (2–4 June 2006). This locality was on a sheltered northern slope of the same ridge as the previous locality. Taxonomic composition of canopy trees was similar in the abundance of *Syzygium*, but the canopy was lower, and mosses and other epiphytes were more abundant. The vegetation appeared to be transitional montane/mossy forest. We had a total of 106 trap-nights at this locality; no mist nets or harp traps were set.

Locality 9—1.8 km S, 1.0 km W Mt. Mingan peak, 1677 m elev., 15.46586°N, 121.39457°E (28–31 May 2006). This locality was centered on an exposed ridge covered with old-growth mossy forest (Fig. 2A). The canopy on the exposed ridge itself was ca. 1 m in height, but taller on more sheltered slopes (ca. 3 m tall), and with emergents of up to 6 m in both cases. Here *Tristaniopsis* was dominant, but *Syzygium* was also common. Many of the trees, including *Elaeocarpus*, *Lithocarpus*, and *Vaccinium*, were stunted. Trunks and branches of most vegetation, as well as exposed sections of the forest floor, were thickly covered by mosses, especially on the sheltered slopes; moss was less abundant on the vegetation on the exposed ridge. We had a total of 37 net-nights, 10 harp-trap-nights, and 821 trap-nights at this locality.

Locality 10—1.5 km S, 0.5 km W Mt. Mingan peak, 1681 m elev., 15.46802°N, 121.40039°E (5–7 June 2006). This locality was on a relatively flat area on the upper eastern slope of Mt. Mingan. Here, the old-growth mossy forest had a higher canopy than that at 1677 m: ca. 5 m, with emergents up to 7 m. The composition of canopy species was similar to that seen at 1677 m, with *Syzygium* predominating, but *Tristaniopsis* was the most prominent emergent. *Pandanus* was common here as well. Climbing pandan and climbing bamboo were particularly abundant, especially toward the ridgetop. Thick mosses and lichens were common on the vegetation and bare ground. We had a total of 916 trap-nights at this locality; we set no mist nets or harp traps.

Locality 11—0.9 km S, 0.3 km W Mt. Mingan peak, 1785 m elev., 15.47390°N, 121.40066°E (1–4 June 2006). This locality was at the highest elevation we could access on Mt. Mingan. The old-growth mossy forest was on a steeper slope than at locality 10, and the forest, although of similar taxonomic composition to the former, had a more stunted canopy (1 m on the exposed ridgetop, and up to 3 m on the flat, sheltered western slope) and shorter emergents (ca. 5 m). The dominant trees were myrtles, including *Leptospermum*, *Syzygium*, and *Xanthomyrtus*, but conifers such as *Dacrycarpus* and *Falcatifolium* were abundant as well. Also common were members of Theaceae, including *Camelia* and *Cleyera*, as well as *Ilex* (Aquifoliaceae). *Freycinetia* vines and climbing bamboo formed dense tangles that choked the vegetation on the exposed ridgetop and rendered the area nearly impassable. The dominance of *Freycinetia* extended up to the peak on the exposed eastern slopes. We had a total of nine net-nights and 596 trap-nights at this locality.

Trapping Procedures

We followed the same procedures employed in our previous surveys of mammals in the Philippines to enable comparisons among study areas in this survey and transects on other mountains and islands (Heaney et al., 1989, 1999, 2006a,b; Heaney, 1991; Rickart et al., 1991, 1993, 2011; Balete et al., 2009; Alviola et al., this volume; Duya et al., this volume).

At each of our survey localities, sampling of mammals was limited to an area within a 50-m elevational range above and below the central elevation, as listed above (see Study Area). Our procedures for the capture and handling of animals in the field followed all laws and regulations of the Philippines.

For surveying bats, we set mist nets close to the ground (ca. 0.5–1 m above ground at the bottom edge) across potential flyways of bats. We also used two locally manufactured harp traps to supplement mist netting. We used both mist nets and harp traps at most localities, but only mist nets at 100, 1476, and 1785 m, and at 1540 m we did not sample bats. We accumulated a total of 103 net-nights and 26 harp-trap-nights, with the latter comprising 29–50% of bat sampling effort at localities where they were used (Table 1).

Our trapping for non-volant small mammals consisted of ground trapping with Victor rat traps (76% of total effort) and arboreal trapping with Museum Special and Victor rat traps (24%). Because trapping above ground was mainly dependent on the availability of lianas and horizontal branches, our arboreal trapping effort varied with the habitat type at our survey localities, ranging from 9% of the total trapping effort in stunted mossy forest at 1785 m to 43% in lowland dipterocarp forest at 559 m (see Study Area). Ground traps were baited either with pieces of roasted coconut coated with peanut butter or with live earthworms (secured on the bait stage with a safety pin); arboreal traps were baited solely with the coconut bait. Trapping with earthworm bait composed 51% of the total ground-trapping effort. Except for locality 1 (100 m), where only coconut bait was used, trapping with earthworm bait accounted for 29% (at 733 m) to 66% (at 1677 m) of the ground trapping effort per locality (Table 3).

Voucher specimens were prepared from all captured animals. In the field, we recorded sex, age, reproductive condition, external measurements (total length, length of tail vertebrae, forearm, hind foot including claws, and ear; mm), and weight (g) for each specimen.

Before a specimen was either fixed in formalin solution (10%) or skeletonized and stored in 95% ethyl alcohol, a small sample of muscle tissue, typically from the thigh, was removed and stored in a cryotube with 95% ethyl alcohol. All specimens were taken to the Field Museum to be cataloged and prepared for study. Fluid specimens were transferred to 70% ethyl alcohol, skeletons were air-dried before being cleaned by dermestid beetles, and tissue samples were stored in liquid nitrogen. The skulls of some fluid specimens were removed and cleaned for identification and taxonomic study. After completion of the study, a portion of the specimens will be deposited at the National Museum of the Philippines.

Table 1. Distribution of bats along an elevational gradient on Mt. Mingan. Netting success for fruit bats (per net-night) is indicated in parentheses after the number of individuals captured. All fruit bats were captured in mist nets; insectivorous bats were captured in mist nets and harp traps, as indicated. S, sighted or reliably reported but not captured.

	No. of individuals captured by locality									
Species	**1 100 m**	**2 559 m**	**3 733 m**	**4 902 m**	**5 1074 m**	**6 1305 m**	**7 1476 m**	**9 1677 m**	**11 1785 m**	**Total**
Fruit bats										
Cynopterus brachyotis	23 (2.30)	4 (0.57)	0	0	0	0	0	0	0	27
Haplonycteris fischeri	0	0	1 (0.25)	0	0	0	0	0	0	1
Otopteropus cartilagonodus	0	0	0	0	0	0	4 (0.33)	11 (0.30)	0	15
Ptenochirus jagori	1 (0.10)	0	0	0	0	0	0	0	0	1
Pteropus/Acerodon/Desmalopex spp.	0	S	S	0	0	0	0	0	0	S
Rousettus amplexicaudatus	1 (0.10)	0	0	0	0	0	0	0	0	1
Insectivorous bats										
Megaderma spasma	0	1[a]	2[a]	0	0	0	0	0	0	3
Coelops hirsutus	0	0	0	0	0	1[b]	0	0	0	1
Hipposideros ater	0	0	0	0	0	0	0	1[b]	0	1
Hipposideros obscurus	0	0	1[a]	0	0	0	0	0	0	1
Rhinolophus cf. *arcuatus*	1[a]	0[c]	0[c]	3[b]	1[b]	1[b]	7[a]	0	0	13
Rhinolophus subrufus	0	0	2[a]	0	0	0	0	0	0	2
Rhinolophus virgo	0	0	1[a]	0	0	0	0	0	0	1
Harpiocephalus harpia	0	1[a]	0	0	0	0	0	0	0	1
Kerivoula whiteheadi	0	0	1[b]	0	0	0	0	0	0	1
Murina cyclotis	0	1[a]	0	0	0	0	0	0	0	1
Murina sp.	0	1[a]	1[a]	0	0	0	0	0	0	2
No. of net-nights	10	7	4	6	6	12	12	37	9	103
Total fruit bats (bats/net-nights)	25 (2.5)	4 (0.57)	1 (0.25)	0 (0)	0 (0)	0 (0)	4 (0.33)	11 (0.30)	0 (0)	45 (0.44)
Total insectivorous bats	1	4	8	3	1	2	7	1	0	27
No. of harp-trap-nights	0	2	2	3	3	6	0	10	0	26
Total no. of species (captured + reported/inferred)	4	5 + 2	7 + 2	1	1	2	2	2	0	16 + 1

[a] Captured in mist net.

[b] Captured in harp trap.

[c] Presence inferred from captures at higher and lower elevations.

We tested for differences between observed and expected numbers of captures of nonvolant small mammals within species among localities using χ^2 tests, with the expected values for a given species based on the percentage of total trapping effort at each locality. We evaluated the patterns of diel activity, bait preference, and location (indicated by trap position) of non-volant small mammals using chi-square tests. Assessment of diel activity was based on expected frequencies of capture adjusted to the approximate length of trapping period: diurnal (10 h) and crepuscular–nocturnal (14 h). Bait preference was assessed with expected frequencies proportional to the total number of trap-nights for the two types of baits we used—coconut or earthworms—but excluding the results of the arboreal trapping, which used only coconut bait. Trap position was assessed with expected frequencies proportional to the number of trap-nights on the ground surface (including slightly raised areas, up to 0.5 m, easily reached from the ground) or above the ground surface (more than 0.5 m aboveground and not easily reached from the ground surface). For one species (*Apomys microdon*), because the sample size was too small to assess with chi-square tests, we assessed diel activity and trap position using the binomial distribution, with the expectation of equal probability of each individual being captured in the relevant period or position. We could not test bait preference for this species because all individuals were trapped arboreally, and only coconut bait was placed on arboreal traps. For all χ^2 tests, we followed the convention of conducting tests only on total samples of 20 or more individuals, with five or more individuals per "treatment" in at least 80% of the treatments (e.g., per elevation or bait type). The relationship of species richness and relative abundance (number of individuals/trap-night) with elevation was assessed using Spearman's coefficient of rank correlation (r_s).

Results

We recorded a total of 35 species of mammals on Mt. Mingan, consisting of one shrew, one macaque, six fruit bats, 11 insectivorous bats, 12 rodents, two civets, one wild pig, and one deer (Tables 1–3). Among the bats, the giant flying foxes (*Acerodon, Desmalopex, Pteropus* spp., or a combination thereof) were not captured, but we observed them at two low elevation localities (559 and 733 m). We also did not capture the northern giant cloud rat (*Phloeomys pallidus*) but observed one individual near 1677 m. All the other large mammals, namely the long-tailed macaque (*Macaca fascicularis*), Malay civet (*Viverra tangalunga*), Philippine warty pig (*Sus philippensis*), and Philippine brown deer (*Cervus mariannus*), were observed

TABLE 2. Distribution of native non-volant small mammals along the elevational gradient on Mt. Mingan; values indicate the number caught at each locality. Boldface indicates captures greater than expected from χ^2 tests based on number of trap-nights at each locality. Number of native species equals documented (plus inferred).

Species	No. of individuals caught by locality											Total	χ^2	*P*
	1 100 m	**2 559 m**	**3 733 m**	**4 902 m**	**5 1074 m**	**6 1305 m**	**7 1476 m**	**8 1540 m**	**9 1677 m**	**10 1681 m**	**11 1785 m**			
Crocidura grayi	0	0	0	0	0	0	1	0[b]	4	0	0	5	—	—
Apomys aurorae	0	0	3	**14**	**9**	**33**	**41**	1	1	0	0	102	140.12	<0.001
Apomys microdon	0	0	0	1	0[b]	3	2	0	0	0	0	6	—	—
Apomys minganensis	0	0	0	0	0	0	0	8	**24**	**37**	**27**	96	138.49	<0.001
Apomys musculus	0	0	0	0	0	0	0	0	1[c]	0	0	1	—	—
Archboldomys sp.	0	0	0	0	0	0	3	0[b]	**9**	**7**	**4**	23	24.35	0.007
Bullimus luzonicus	0	3	0[b]	3	3	8	3	1	2	0	0	23	—	—
Chrotomys sp.	1	0	0	0	0	0	0	0	0	0	0	1	—	—
Rattus everetti	0	**3**	**5**	2	1	**11**	5	4	1	2	0[d]	34	39.56	<0.001
Rattus exulans[a]	3	0	0	0	0	0	0	0	0	0	0	3	—	—
Rattus tanezumi[a]	4	0	0	0	0	0	0	0	0	0	0	4	—	—
Rhynchomys sp.	0	0	0	0	0	0	2	0[b]	**6**	**11**	**4**	23	32.36	<0.001
Total captures	8	6	8	20	13	**55**	**57**	14	**48**	**57**	35	321	50.62	<0.001
Total trap-nights (ground)	198	255	297	297	300	545	672	106	674	626	542	4512		
Total trap-nights (arboreal)	0	192	120	140	102	162	100	0	147	68	54	1085		
No. of native species	1	2	2 (+1)	4	3 (+1)	4	7	4 (+3)	8	4	4	10		
No. of non-native species	2	0	0	0	0	0	0	0	0	0	0	2		

[a] Non-native species.

[b] Presence inferred from occurrence at higher and lower elevations.

[c] Hand-caught.

[d] Observed at the locality but not captured.

either directly by us or by local people we interviewed during our survey.

Fruit Bats

We captured 45 individuals of five species of fruit bats in a total of 103 net-nights (Table 1). Two species comprised the majority of captures, with the short-nosed fruit bat (*Cynopterus brachyotis*) accounting for more than 50% and the Luzon pygmy fruit bat (*Otopteropus cartilagonodus*) for more than 30%. The rest, including Philippine pygmy fruit bats (*Haplonycteris fischeri*), musky fruit bats (*Ptenochirus jagori*), and common rousettes (*Rousettus amplexicaudatus*), were caught in numbers too low to allow reliable estimates of their relative abundance and distribution along the gradient. As shown in Table 1, fruit bat diversity (83%), including the observed flying foxes, was concentrated in the lowland habitats (100–733 m). The most abundant of the fruit bats (1.59 bats/net-night; Table 1), *C. brachyotis,* was limited to the two lowest elevation sampling localities (100 and 559 m). The only records of *P. jagori* and *R. amplexicaudatus* were at 100 m, and *H. fischeri* was recorded only at 733 m. The second most abundant fruit bat (0.31 bats/net-night; Table 1), *O. cartilagonodus*, was the only species of fruit bat recorded in lower montane forest (1476 m) and upper montane forest (1677 m), with roughly equal abundance at the two elevations.

Insectivorous Bats

In contrast to the fruit bats, insectivorous bats made up the majority of overall bat species richness on Mt. Mingan (65% of the captured species) but accounted for just a little more than a third of the total individuals captured (28 individuals or 38% of total; Table 1). Their highest concentration, in terms of individuals captured, was likewise in the lowlands (100–733 m), where nine of 11 species (82%) were captured. However, the Philippine tailless roundleaf bat, *Coelops hirsutus*, was recorded only in lower montane forest at 1305 m, and the dusky roundleaf bat, *Hipposideros ater*, was documented only in the upper montane forest at 1677 m. We captured a specimen each of a small tube-nosed bat (*Murina* sp.) at 559 and 733 m, currently unidentified to species. Among all bat species, the arcuate horseshoe bat, *Rhinolophus arcuatus*, had the widest elevational distribution, ranging from 100 m in a mixed reforestation/agricultural area to 1476 m in primary lower montane forest, and appeared to be most abundant at the middle and upper elevations (Table 1).

Non-volant Small Mammals

We documented 12 species of nonvolant small mammals on Mt. Mingan, consisting of one native shrew, nine native murid rodents, and two alien commensal murid rodents (Table 2). Our record of the shrew-rat *Rhynchomys* was the first of this Luzon endemic genus in the Sierra Madre. Three species we captured were previously unknown and appear to be endemic to the Mingan Mountains: *Apomys aurorae* and *A. minganensis* (Heaney et al., this volume) and a new species of shrew-mouse (*Archboldomys*; D. S. Balete, unpubl. data); the *Rhynchomys* might also be new and is under study. All but one of the native non-volant small mammals were restricted to localities in native forest (559 m and higher).

Species richness of native non-volant mammals was lowest in the lowlands at 100 and 559 m (1 or 2 species) and highest (8 species) in mossy forest at 1677 m (Fig. 3; Table 2). Above 1677 m, the number of species dropped sharply to four, the

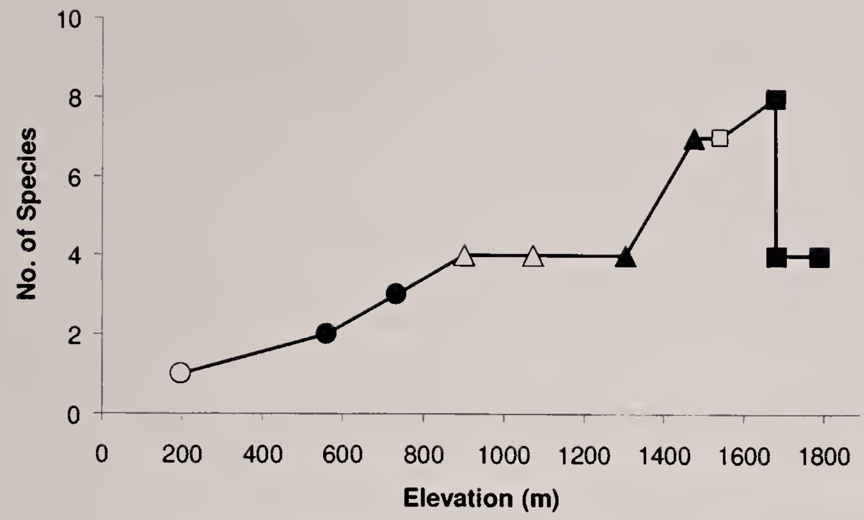

FIG. 3. Species richness of native non-volant small mammals at study areas along the Mt. Mingan elevational transect, indicating the habitat type in each (see Study Area for details): reforestation/agricultural area (**open circle**), lowland dipterocarp forest (**solid circle**), transitional lowland dipterocarp/montane forest (**open triangle**), montane forest (**solid triangle**), transitional montane/mossy forest (**open square**), and mossy forest (**solid square**).

same as at our montane study areas. The striped shrew-rat (*Chrotomys* sp.) was the only native species found in a mixture of reforestation and agricultural areas at 100 m, where it occurred sympatrically with the two non-native commensal rodents, *Rattus exulans* and *R. tanezumi.* These three species were not recorded anywhere else on our gradient. We documented or inferred three native species in relatively intact lowland dipterocarp forest: at 559 m, the large Philippine forest rat (*Bullimus luzonicus*) and the common Philippine forest rat (*R. everetti*), and at 733 m, these two (documented or inferred) plus one of the newly discovered species of forest mouse (*A. aurorae*). In addition to these three species, we recorded the small Luzon forest mouse (*A. microdon*) in the transitional lowland dipterocarp/montane forest at 902 m and inferred its presence at 1074 m. The same four native species found at 902 and 1074 m were recorded at 1305 m in primary montane forest.

At the next higher elevation (1476 m), but still in primary montane forest, species richness increased sharply to seven species (Table 2). In addition to the four species present between 559 and 1305 m, we recorded the Luzon shrew (*Crocidura grayi*), a shrew-mouse (*Archboldomys* sp.), and a shrew-rat (*Rhynchomys* sp.). At 1540 m, in transitional montane/mossy forest, we recorded a total of four species, including three of the species found at lower elevations (*A. aurorae*; *B. luzonicus*, and *Rattus everetti*) and the second newly discovered forest mouse (*A. minganensis*). We inferred the presence of three additional species (*C. grayi*, *Archboldomys* sp., and *Rhynchomys* sp.) that were recorded both above and below this locality. The only other location where the two morphologically similar large *Apomys* (*A. aurorae* and *A. minganensis*) co-occurred was at 1677 m in mossy forest. It was here that we found the highest species richness of non-volant small mammals on Mt. Mingan (8 species), including one specimen of the least Luzon forest mouse (*A. musculus*) caught by hand.

A sharp decline in species richness was documented at 1681 and 1785 m, our uppermost study areas in mossy forest (Fig. 3; Table 2), where we recorded four species (*A. minganensis*, *Archboldomys* sp., *R. everetti*, and *Rhynchomys* sp.), three of which are endemic to the Mingan Mountains.

Among the 10 species of native non-volant mammals from our transect, only three were habitat/elevational generalists (Table 2). Both *B. luzonicus* and *R. everetti* occurred from lowland dipterocarp forest at 559 m to mossy forest at 1681 m (for the former), and to 1785 m (for the latter). *Apomys aurorae* was documented from 733 m in lowland dipterocarp forest up to 1677 m in mossy forest. *Apomys microdon* occurred in transitional lowland dipterocarp/montane forest at 902 m to lower montane forest at 1476 m. *Apomys musculus* and *Chrotomys* sp. had the narrowest elevational ranges: we captured the former only at 1677 m and the latter only at our 100-m locality in heavily disturbed habitat.

Five native species were found only in forest above 1305 m (Table 2). Two of these, *Rhynchomys* sp. and *Archboldomys* sp., ranged from primary lower montane forest at 1476 m to upper montane forest at 1785 m. *Apomys minganensis* overlapped with them completely from 1546 m to the top of the transect, whereas *C. grayi* was found from 1476 to 1677 m. The fifth species, *A. musculus*, was found only in mossy forest at 1677 m, where a single individual was hand-caught in a ball-shaped nest of dry *Freycinetia* and climbing bamboo (*Schizostachyum*) leaves tucked in the axil of a *Pandanus* leaf, ca. 1.5 m above ground.

If we exclude data from 1540 m, because of low trapping effort, two species (*R. everetti* and *A. aurorae*) were documented in greater abundance (as number of individuals/100 trap-nights) than expected in montane forest at 1476 m or below, and *B. luzonicus* showed a similar pattern but was not statistically significant because of low sample size (Table 2). Similarly, the abundance of three other species (*A. minganensis*, *Archboldomys* sp., and *Rhynchomys* sp.) was higher than expected in mossy forest at 1677, 1681, and 1785 m (Table 3).

Across the transect, earthworm bait was generally more effective than coconut bait (Tables 3, 4). This was most evident in montane and mossy forest above 1305 m, where four of the most abundant species (*A. aurorae*, *A. minganensis*, *Archboldomys* sp., and *Rhynchomys* sp.) showed significant preference for earthworm bait. Only *B. luzonicus* and *R. everetti* showed significant preference for coconut bait. The species that did not show a significant bait preference (*C. grayi*, *A. microdon*, *Chrotomys* sp., *R. exulans*, and *R. tanezumi*) generally had low sample sizes. Trap success using earthworm bait increased significantly with increasing elevation (r_s = 0.733, d.f. 7, P = 0.02), but trap success using coconut bait did not vary significantly (r_s = −0.067, d.f. 7, $P > 0.05$; Table 3).

Six species (*A. aurorae*, *A. microdon*, *A. minganensis*, *B. luzonicus*, *Rattus everetti*, and *Rhynchomys* sp.) had significantly more captures during the crepuscular/nocturnal period than during daylight (Table 4). *Archboldomys* sp. was the only species that appeared to be active both day and night. This species accounted for 63% of the total daytime captures, but we also recorded it in nearly equal numbers at night (Table 4). The remaining species were captured too infrequently for statistical analysis. Overall, an increasing percentage of diurnal captures was positively correlated with increasing elevation (r_s = 0.738, d.f. 7, P = 0.02; Table 3).

Seven nonvolant species showed significant patterns of capture on the basis of trap position (Table 4). *Apomys microdon* was exclusively arboreal. The remaining native species were caught almost exclusively on the ground in significant to highly significant numbers. Too few *C. grayi*, *R.*

Table 3. Summary of overall capture frequencies by bait type and diel period of all native non-volant small mammals along an elevational gradient on Mt. Mingan. Captures greater than expected from χ^2 tests of ground-traps with the two types of bait are given in boldface. Correlation between elevation and captures or overall trap success is indicated by Spearman's correlation, r_s. Brackets indicate data that were excluded from statistical tests because of low sampling effort (see Methods).

	Capture frequency by locality												
	1 **100 m**	**2** **559 m**	**3** **733 m**	**4** **902 m**	**5** **1074 m**	**6** **1305 m**	**7** **1476 m**	**8** **1540 m**	**9** **1677 m**	**10** **1681 m**	**11** **1785 m**	**Totals**	r_s
Coconut bait (ground)													
Trap nights	[198]	133	212	133	154	295	365	[58]	228	336	205	2061	
Captures	[8]	**6**	5	**9**	**8**	20	18	[6]	5	19	7	97	
Captures/100 trap-nights	[4.04]	4.51	2.36	6.77	5.19	6.78	4.93	[10.34]	2.19	5.65	3.41	4.71	−0.067
Earthworm bait (ground)													
Trap nights	[0]	122	85	164	146	250	307	[48]	446	290	337	2147	
Captures	[0]	0	**3**	10	5	**31**	**39**	[8]	**42**	**38**	**28**	**196**	
Captures/100 trap-nights	—	0	3.53	6.1	3.42	12.4	12.7	[16.67]	9.42	13.1	8.31	9.12	0.733
χ^2	—	5.50	0.31	0.05	0.54	4.57	11.87	—	11.29	9.48	4.73	29.54	
P	—	0.019	0.578	0.821	0.462	0.032	<0.001	—	<0.001	0.002	0.03	<0.001	
Overall trap success (%)													
Weighted	[4.04]	2.35	2.69	6.40	4.33	9.36	8.48	[13.20]	6.97	9.1	6.46	6.88	0.700
Unweighted	[2.02]	2.26	2.94	6.43	4.3	9.59	8.82	[13.50]	5.8	9.38	5.86	6.82	0.567
Diel period													
Diurnal	[0]	0	0	1	0	0	3	[0]	10	2	3	19	
Nocturnal/ crepuscular	[8]	6	8	19	13	55	54	[14]	37	55	32	279	
Percent diurnal	[0]	0	0	5	0	0	5.3	[0]	21.3	3.5	8.6	6.4	0.738
Coconut bait	[0]	192	120	140	102	162	100	[0]	147	290	54	1307	
(arboreal)	[0]	0	0	1	0	4	2	[0]	0	0	0	7	
(% arboreal)	[0]	0	0	0.71	0	2.47	2	—	0	0	0	0.64	−0.078

exulans, and *R. tanzumi* were caught to test statistically, but all were caught on the ground.

Large Mammals

The large mammals that we documented directly or were reported to us by local people are found throughout northern Luzon: the long-tailed macaque (*Macaca fascicularis*), northern giant cloud rat (*Phloeomys pallidus*), palm civet (*Paradoxurus hermaphroditus*), Malay civet (*Viverra tangalunga*), Philippine warty pig (*Sus philippensis*), and Philippine brown deer (*Cervus mariannus*). Signs of macaques, consisting mainly of erect palms (*Pinanga*) and pandan (*Pandanus*) with freshly removed tender shoots (hearts), were abundant along the trail, particularly from around the transitional lowland dipterocarp/montane forest at 902 m up to mossy forest on top of ridges at 1681 m. We observed wild pig diggings on the ground throughout our transect and saw signs of deer grazing on ferns and other ground-level vegetation in montane and mossy study areas from 1300 to 1785 m. Our only specimen of *P. hermaphroditus* is the partial skull and skeleton of an individual caught in a snare in montane forest at ca. 1300 m. Near our study areas at 1540 m, we observed one individual of *P. pallidus* at night, ca. 10 m up a tree, feeding on tender young leaves. On the basis of information gathered from both lowland farmers and indigenous Dumagats, who hunt these large mammals for food, all of these species are currently common in the Mingan Mountains.

Discussion and Conclusions

Adequacy of Sampling

Bats—The five species of fruit bats we captured comprised close to a third (31%) of the total diversity of bats we recorded on Mt. Mingan, but nearly two-thirds (62%) of the individuals (Table 1). However, our netting effort averaged fewer than 10 net-nights/study area and our capture of fruit bats was too low (45 total) to allow more than crude approximations of their diversity, distribution, and abundance (Heaney et al., 1989, 1999, 2006b; Heideman & Heaney, 1989).

We also recorded 11 species of insectivorous bats (Table 1). This compares favorably with the 15 species previously known in the entire northern Sierra Madre (Duya et al., 2007) and is the greatest number from any single mountain in the Sierra Madre surveyed thus far. The present study added four more species to the list for the Sierra Madre: *Megaderma spasma*, *Rhinolophus subrufus*, *Kerivoula whiteheadi*, and *Murina* sp. However, we did not encounter eight of the species previously known in the Sierra Madre: *Hipposideros diadema*, *R. inops*, *R. philippinensis*, *K.* cf. *papillosa*, *Myotis horsfieldi*, *M. muricola*, *Pipistrellus javanicus*, and *Chaerephon plicatus*. As with the fruit bats, our mist netting and harp-trapping effort was low (averaging fewer than 10 net-nights and fewer than 3 harp-trap-nights per survey locality, respectively), and our capture rates of insectivorous bats were too low to have thoroughly sampled the fauna or to allow statistical analyses.

TABLE 4. Summary of captures of 11 species of non-volant small mammals by bait type, diel period, and trap position on Mt. Mingan. Captures per 100 trap-nights are indicated in parentheses. Captures greater than expected from χ^2 test are shown in boldface (except as noted; see Methods).

		Bait type		Diel period		Trap position	
Species	Total trapped	Coconut	Earthworm	Nocturnal/crepuscular	Diurnal	Ground surface	Above ground
Crocidura grayi	5	2 (0.34)	3 (0.40)	5	0	5	0
Apomys aurorae	96	22 (2.66)	**74**[b] (6.60)	**94**[b]	2	**96**[b]	0
Apomys microdon	6	6[c] (1.49)	—	**6**[d]	0	0	**6**[d]
Apomys minganensis	102	29 (1.84)	**73**[b] (5.05)	**99**[b]	3	**102**[b]	0
Archboldomys sp.	23	4 (0.35)	**19**[b] (1.38)	11	12	**23**[e]	0
Bullimus luzonicus	23	**17**[b] (1.24)	5 (0.34)	**22**[b]	1	**22**[e]	1
Chrotomys sp.	1	1 (0.50)	0	1	0	1	0
Rattus everetti	34	**27**[b] (1.41)	7 (0.38)	**34**[b]	0	**34**[b]	0
Rattus exulans[a]	3	3 (1.52)	0	3	0	3	0
Rattus tanezumi[a]	4	4 (2.02)	0	4	0	4	0
Rhynchomys sp.	23	0	**23**[b] (1.67)	**22**[b]	1	**23**[e]	0

[a] Nonnative species.

[b] $P < 0.01$.

[c] Only coconut bait was used on arboreal traps.

[d] Significance determined from binomial distribution.

[e] $P < 0.05$.

NON-VOLANT SMALL MAMMALS—Our total trapping effort consisted of 4512 ground trap-nights and 1085 arboreal trap-nights. Except for our study areas at 100 and 1540 m, where fewer traps were set, ground trapping effort ranged from 255 to 300 trap-nights, in lowland dipterocarp forest (540 and 733 m) and transitional lowland dipterocarp/montane forest (902 and 1074 m), and from 542 to 674 trap-nights, in montane forest (1305 and 1476 m) and mossy forest (1677 to 1785 m; Tables 2, 3). Arboreal trapping ranged from 54 to 192 trap-nights per locality (Table 2).

As shown in Figure 4A, the species accumulation curves in all study areas approached an asymptote, except that for 1476 m. The trapping effort at 100 m was less than 200 trap-nights, but because the area was dominated by non-native mahogany and coffee, we did not expect to record any native species other than a striped shrew rat, *Chrotomys* sp., which has often been taken in agricultural areas (e.g., Rickart et al., 2005, 2011). We accumulated 300 trap-nights at 1074 m, and we did not expect additional species with further ground trapping, except possibly *A. microdon*, which also occurred at 902 and 1305 m, although it was taken there only by arboreal traps. A cumulative plot for all localities (Fig. 4B) shows progressive increase in species richness up to about 3000 trap-nights as we sampled at increasing elevation, followed by a plateau from 3000 to 5000 trap-nights across three sites. It is possible that additional trapping would have increased the number of species at individual study areas, but we hypothesize that further trapping will not change the number of species recorded for the entire mountain.

Mammals of Mt. Mingan and the Sierra Madre Mountain Range

Previously, the Sierra Madre Range was reported to have a total of 48 species of native mammals (1 shrew, 10 fruit bats, 23 insectivorous bats, 9 murid rodents, 1 macaque, 2 viverrid carnivores, 1 wild pig, and 1 deer), along with one non-native shrew and two non-native rodents (Heaney et al., 1998; Duya et al., 2007). Our survey on Mt. Mingan added new records of an unidentified tube-nosed bat (*Murina* sp.) and four previously unknown species of native murid rodents that may be locally endemic: two forest mice (*A. aurorae* and *A. minganensis*; Heaney et al., this volume), one shrew-mouse (*Archboldomys* sp.), and one shrew-rat (*Rhynchomys* sp.). The mammal fauna of Mt. Mingan is the richest of any of the surveyed mountains in the Sierra Madre, with 33 native mammals (Tables 1, 2; Danielsen et al., 1994; Duya et al., 2007, this volume). With at least 10 species (83%) of non-volant small mammals endemic to Luzon, four of which are restricted to the Mingan Mountains, we believe that this portion of the Sierra Madre constitutes a highly distinctive center of mammalian endemism.

Our capture of five species of fruit bats is only half of what was previously reported for the Sierra Madre (Heaney et al., 1998; Duya et al., 2007). Although we observed several flying foxes at our lowland sites, we were unable to identify them. Four species are known to occur in other parts of the Sierra Madre, including *Acerodon jubatus*, *Desmalopex leucopterus*, *Pteropus hypomelanus*, and *P. vampyrus* (Heaney et al., 1998; Duya et al., 2007; Esselstyn et al., 2008). These species are not easily captured by mist nets and are thus difficult to document. Several species were notably missing from our records on Mt. Mingan. *Macroglossus minimus* is a widespread species commonly associated with wild and domestic bananas (*Musa* spp.), both of which were conspicuously absent from the Mingan transect. Other Luzon species that we did not record were two large fruit bats associated with more intact and higher elevation forest habitats (*Dyacopterus rickarti* and *Harpyionycteris whiteheadi*) and two cave-dwelling fruit bats (*Eonycteris spelaea* and *E. robusta*). These four species have not been reported in other parts of the Sierra Madre Range (Heaney et al., 1998; Duya et al., 2007). Elsewhere on Luzon, *D. rickarti* has been reported only from Abra Province, on the western side of the Cordillera range (Helgen et al., 2007), and *H. whiteheadi* only on Mt. Isarog, in southeastern Luzon (Heaney et al., 1999); both of these large bats are widespread in the central and southern Philippines (Heaney et al., 1998).

Our record of 11 species of insectivorous bats in the Mingan Mountains constituted nearly half of the 25 known species in the Sierra Madre Range (Heaney et al., 1998; Duya et al., 2007), and Mt. Mingan has higher species richness than any other single mountain in the range (Duya et al., 2007). Among the species recorded in other parts of the Sierra Madre, many

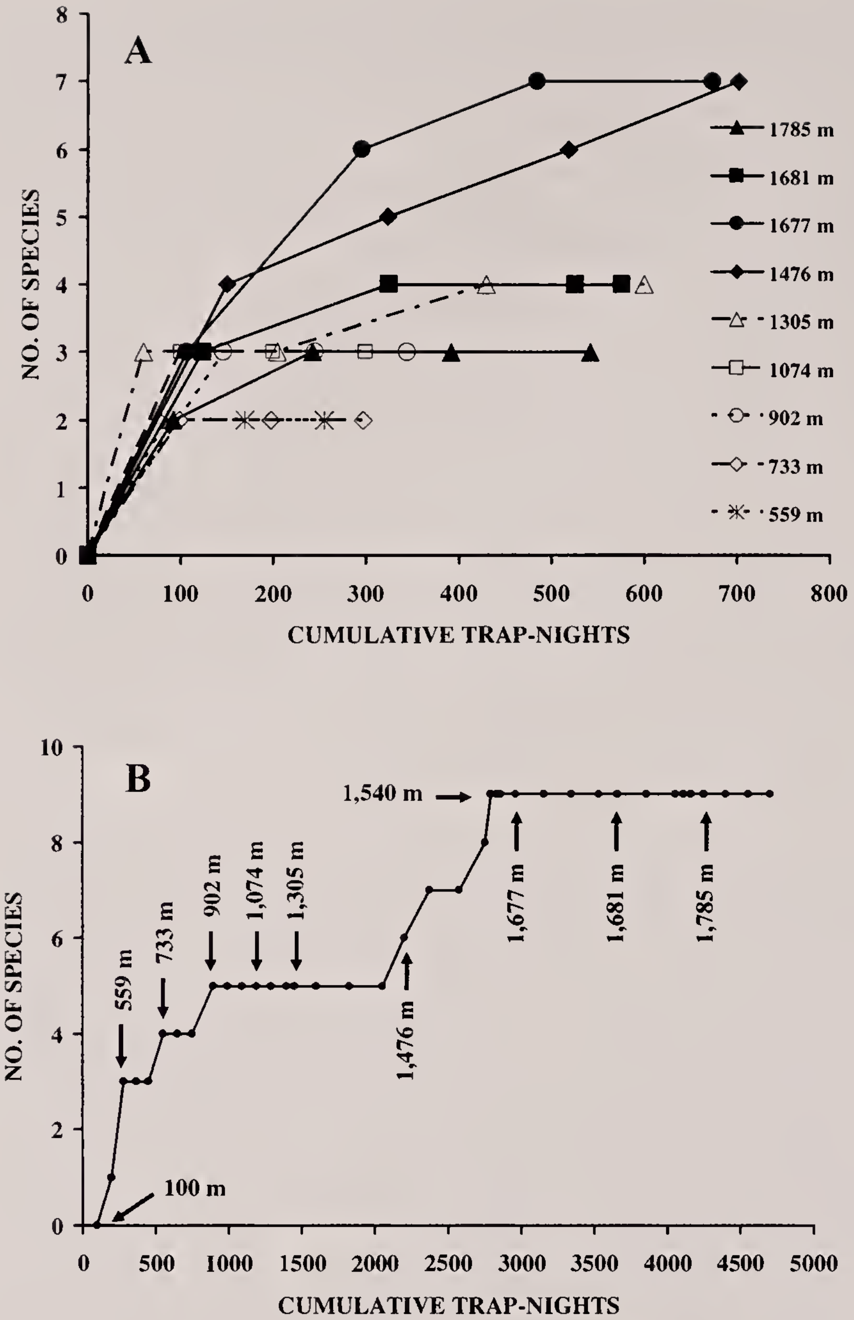

Fig. 4. Species accumulation curves for native non-volant small mammals on Mt. Mingan (**A**) in individual study areas and (**B**) on the entire transect. Locality 1 (100 m) is not plotted in panel A because of small sample size. **Arrows** in panel B indicate the initiation of trapping at corresponding study locations. Habitat types along the transect include lowland dipterocarp forest (559 and 733 m), transitional lowland/montane forest (902 and 1074 m), montane forest (1476 and 1540 m), and mossy forest (1677, 1681, and 1785 m).

we failed to capture on Mt. Mingan were those associated with caves and forest over limestone, including *Hipposideros diadema*, *H. lekaguli*, *Rhinolophus inops*, *R. philippinensis*, *Miniopterus schreibersii*, and *Chaerephon plicatus* (Heaney et al., 1998; Duya et al., 2007). Others were small vespertilionids that are typically difficult to capture with mist nets, including pipistrelles (*Pipistrellus* spp.) and myotis (*Myotis* spp).

The addition of an apparently new species of *Rhynchomys* to the endemic mammal fauna of the Sierra Madre Range completes the representation of the "earthworm-mouse" clade (Jansa et al., 2006; shrew-mice and shrew-rats) on the eastern side of Luzon, together with *Apomys*, *Archboldomys*, and *Chrotomys*. We now know that this group is widespread throughout Luzon. However, outside of the Central Cordillera, Mt. Mingan and Mt. Isarog are the only mountains that support species of all four genera of this clade, and Mt. Mingan is so far the lowest mountain to support members of all four genera (Rickart et al., 1991, 2011; Heaney et al., 1998, 1999, 2003).

As is evident from our results, Mt. Mingan, in particular, and the Sierra Madre, in general, support fewer of the Luzon endemic non-volant mammal species than does the Central Cordillera. Most notably, the Central Cordillera supports members of all five genera in the cloud rat clade, including *Batomys* and *Carpomys* (2 species of each), *Musseromys* sp., *Crateromys schadenbergi*, and *Phloeomys pallidus* (Heaney et al., 1998, 2003; Rickart et al., 2011). The last of these is the only member of the cloud rat clade documented in the Sierra Madre Range. Elsewhere on Luzon, Mt. Isarog (1966 m) supports two representatives of the cloud rat clade, *P. cumingi* and *Batomys granti* (Heaney et al., 1999), as does Mt. Banahaw (2177 m), with *P. pallidus* and *Musseromys gulantang* (Rosell, 1996; Heaney et al., 2009). Other mountains on Luzon that we surveyed each support only one species of *Phloeomys*.

Two other species that were first recorded in the Cordillera also remain undocumented anywhere in the Sierra Madre: *Abditomys latidens* and *Tryphomys adustus*. Further surveys are needed to determine whether any of these "missing" taxa are present in poorly sampled habitats in the Sierra Madre Range, including intact lowland dipterocarp forest, forest over limestone, ultramafic forest, and high-elevation mossy forest.

Elevational Patterns

Our trapping data indicated that species richness of native non-volant small mammals on Mt. Mingan (Table 2) is positively correlated with elevation (r_s = 0.607, d.f. 9, $P <$ 0.05). However, the relationship is not linear; the number of species increases from the lowland study areas (100–733 m) to mossy forest (1677 m) and then declines above that (Fig. 3). This is consistent with the pattern of non-volant small mammal distribution revealed by other gradient studies on Luzon, including Mt. Isarog (1966 m), Mt. Tapulao (2037 m), and Mt. Bali-it, Balbalasang (2238 m), as well as on Mindanao (Heaney & Rickart, 1990; Rickart et al., 1991, 2011; Heaney et al., 1999, 2003, 2006; Balete et al., 2009), in which species richness peaks at about 1800–2100 m, corresponding to the transition zone from montane to mossy (= upper montane) forest. Gradient studies outside of the Philippines have shown similar peaks of species richness at mid-elevation (e.g., Md. Nor, 2001; Rickart, 2001; Sanchez-Cordero, 2001; Andrianjakarivelo et al., 2005; McCain, 2007; Stanley & Hutterer, 2007). Rickart et al. (2011) suggest that this pattern is not solely a function of elevation but is influenced by habitat type and topography as well; other possible factors that could influence this pattern, such as temperature, precipitation, competition, and predation, are explored in Heaney (2001).

Our data also indicate that the proportion of endemic species increases with increasing elevation in the Mingan Mountains. Of the native species captured at the lowest elevations (100 and 559 m), one (*Rattus everetti*) is widespread on Luzon, and the other (*Chrotomys* sp.) is probably also widespread, but its identity remains uncertain (E. A. Rickart, unpubl. data). Species present from 733 to 1074 m include one endemic species (*A. aurorae*) and three widespread Luzon species. The eight species present from 1074 to 1540 m include four Mingan endemic species (Table 2). Four species are present at the highest locality, 1785 m, three of which are endemic to the Mingan Mountains. Overall, this pattern suggests a low number and proportion of endemic species in both disturbed and undisturbed lowland forest, with much higher numbers and proportions in montane and mossy forest, as noted in prior studies of Philippine small mammals (e.g., Rickart et al., 1991, 2011; Heaney et al., 2003, 2006; Balete et al., 2009).

That Mt. Mingan (1901 m) supports 10 species of native, non-volant small mammals is consistent with the pattern of a significant positive correlation between maximum elevation and species richness on mountains on Luzon (Rickart et al., 2011), including Mt. Palali (7 species, 1707 m; Alviola et al., this volume), Mt. Isarog (8 species, 1966 m; Rickart et al., 1991; Balete & Heaney, 1997; Heaney et al., 1999), Mt. Tapulao (9 species, 2037 m; Balete et al., 2009), and Mt. Bali-it, Balbalasang (13 species, 2238 m; Heaney et al., 2003).

Finally, we note that two pairs of similar species of forest mice (*Apomys* spp.) occur along the elevational gradient on Mt. Mingan. *Apomys aurorae* and *A. minganensis* are closely related, ground-living species of large body size (Heaney et al., this volume), whereas *A. microdon* and *A. musculus* are closely related arboreal species of small body size. In each species pair, the one listed first occurs at lower elevation and the second at higher elevation, although with some overlap between *A. aurorae* and *A. minganensis*. This implies the possible existence of competition and elevational partitioning between the members of each of these pairs, a topic that deserves further investigation. It should be noted that in neither pair are the species sister-taxa; rather, they are members of species groups that occur widely on Luzon and in some other parts of the Philippines (Steppan et al., 2003; Heaney et al., this volume).

Conservation

The habitat diversity of the Sierra Madre Range is one of the highest on Luzon, and this range is recognized as one of the most important biodiversity areas in the Philippines (CEPF, 2001; Mallari et al., 2001; Ong et al., 2002). Efforts made during the past two decades to protect and manage this area have focused on the northern block, resulting in more than 700,000 hectares of forest with fully legislated protected area status—the largest single network of protected areas within a center of endemism and biodiversity in the Philippines (PAWB, 2004). The results of the present mammal survey indicate an even richer center of mammalian diversity in the Mingan Mountains, in the central section of the Sierra Madre Range. However, this small range is not yet part of any protected area: Aurora National Park (ca. 5676 ha), the only national park in Aurora Province, is located further northeast, outside of the Mingan Mountains (Mallari et al., 2001). Thus, the protection and management of the unique mammalian diversity of the Mingan Mountains is a major conservation challenge in the context of conserving the maximum biodiversity in the Sierra Madre Range.

On the basis of the data generated by our survey, we recognize the following categories of vulnerability for the mammals of the Mingan Mountains (see Heaney et al. 1999, 2006b):

1) Some species subject to unregulated hunting activities have declining populations or have undergone local extinction in some parts of their range, including the giant fruit bats (*Acerodon jubatus*, *Desmalopex leucopterus*, and *Pteropus spp.*), giant cloud rats (*Phloeomys* spp.), macaques (*Macaca fascicularis*), civets (*Paradoxurus hermaphroditus* and *Viverra tangalunga*), wild pig (*Sus philippensis*), and deer (*Cervus mariannus*). On the basis of our interviews of local informants, all these species are exploited for food on Mt. Mingan, although the level of exploitation appeared to be moderate and the number of hunters low. However, we recommend that for productive local management of this resource, hunting activities should be undertaken according to traditional practices and mainly by indigenous peoples for family consumption, not for trade or for sale. Although lowland dipterocarp forest above 500 m remains relatively intact in the Mingan Mountains, areas below 500 m have undergone extensive conversion into farms and residential areas. Although species in this category may tolerate some level of disturbance of their habitats, they are unlikely to survive the complete loss of lowland forest or intensive hunting pressure. We believe that the protection of the remaining lowland forest will be the single most important conservation measure for Mt. Mingan and its associated biodiversity because of its vulnerability to human encroachment.
2) Species that are mainly mid- to high-elevation specialists, including those endemic to the mountain, such as *Otopteropus cartilagonodus*, *Coelops hirsutus*, *Apomys aurorae*, *A. minganensis*, *A. microdon*, *A. musculus*, *Archboldomys* sp., and *Rhynchomys* sp., are associated on Mt. Mingan with montane and mossy forest, habitats that are not presently under any threat. However, we recommend that to ensure the continued survival of these species, as well as species that range more widely across habitats and elevations, these habitats must be protected from future disturbance.
3) Some species are widespread and are not threatened. Most of the remaining species of insectivorous bats, the shrew (*Crocidura grayi*) and some rodents (e.g., *Rattus everetti*) are found in many parts of the Philippines and are more tolerant of habitat disturbance than are those in the previous categories. Some native species that are lowland forest specialists, including certain fruit bats (*Haplonycteris fischeri* and *Ptenochirus jagori*) and murid rodents (e.g., *Chrotomys* sp.) probably are not directly exploited by people. However, some of these are poorly known and were caught in low numbers, especially the insectivorous bats, making it difficult to make definitive assessments of their status. We recommend further research to address this gap and to ensure a more comprehensive management plan for Mt. Mingan.

We conclude that the Mingan Mountains support a remarkable diversity of mammals and represent a center of mammalian endemism distinct from the rest of the Sierra Madre Range. The rich diversity of this fauna is clearly dependent on the equally diverse habitats found on Mt. Mingan. Although the representatives of forest habitats from lowland dipterocarp forest at ca. 500 m up to mossy forest at 1785 m remain relatively intact, the continuing degradation and conversion of the lowland forest below 500 m is of serious concern. Although populations of the native small mammals of Mt. Mingan are likely stable and secure, larger mammals are commonly exploited for food in an unmanaged manner. We therefore strongly recommend the protection of this important biodiversity area and the sustainable management of its resources for the benefit of present and future generations of Filipinos.

While clearly recognizing the importance of this small mountain range to the maintenance of biodiversity of the country, our recommendation for the protection of this mountain is anchored heavily in our belief that the future economic and social well-being of the local communities around Mt. Mingan and outlying regions at large (Aurora, Cagayan, and Nueva Ecija provinces) depend in large measure on the protection of this watershed and native fauna that it supports.

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Chapter 4: Diversity of Small Mammals in Montane and Mossy Forests on Mount Cetaceo, Cagayan Province, Luzon

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Abstract

We surveyed non-volant mammals in montane (1300 and 1400 m) and mossy forest (1500 and 1550 m) on Mount Cetaceo in the northern Sierra Madre of northeast Luzon in 2004 and 2005. We recorded a total of 12 species of mammals, including one shrew (Soricidae), seven murid rodents (Muridae), one deer (Cervidae), one wild pig (Suidae), one macaque (Cercopithecidae), and one civet (Viverridae). In this paper, we present the first ecological data on two recently discovered species endemic to northeast Luzon, *Archboldomys musseri* and *Apomys sierrae*. We captured only three species at 1300 m; captured five species at 1400 m; captured or inferred six species at 1500 m; and documented four species at 1550 m. Combined with an earlier study at 960 m (3 species), these results imply that species richness might increase from the lowlands to ca. 1500 m. The small number of sampling localities prevented strong statistical inference, but percent trap success with roasted coconut bait declined with increased elevation along our short transect, and trap success with live earthworm bait increased along the transect, so that overall trap success varied little along the transect. The most abundant species, *A. sierrae*, significantly preferred earthworm bait and was significantly more abundant in mossy forest than in montane forest. The percentage of diurnal captures along the transect increased with increased elevation, from a low of 0% at 1300 m to nearly 11% at 1550 m, even though no species showed significantly more diurnal than nocturnal/crepuscular activity. These patterns are similar to those on other mountain peaks on Luzon. The number of native species recorded on Mt. Cetaceo (7), plus one species recorded in the nearby lowlands, is similar to the number expected on the basis of the peak elevation of Mt. Cetaceo, supporting the hypothesis that the diversity of small mammals on a given mountain on Luzon is correlated with the elevation of the peak. Large mammals on Mt. Cetaceo are actively hunted; because they use both lowland and montane/mossy forest habitats, they may be threatened by the combination of agricultural expansion in the lowlands and unregulated hunting.

Introduction

The Philippine archipelago is remarkable for its high mammalian diversity and endemism, with more than 185 species of terrestrial mammals documented, of which at least 65% are endemic to the country. This exceptional diversity and endemism are attributed to the country's archipelagic setting, in which many islands and, within large islands, many individual mountains or mountain ranges support unique assemblages of terrestrial mammals. Luzon, the largest and oldest island in the country (Hashimoto, 1981; Hall, 2002), supports at least 43 native species of mammals, of which 35 (81%) are endemic. Many of these Luzon endemics are limited to small parts of the island, specifically including the Central Cordillera of northern Luzon, the Zambales Mountains of west-central Luzon, Mt. Banahaw of central Luzon, and the Mingan Mountains and the northern Sierra Madre in the northeastern portion of the island (Heaney, 1986; Heaney et al., 1998, 2009, this volume: fig. 3; Rickart et al., 1998; Catibog-Sinha & Heaney, 2006; Balete et al., 2007, 2009, this volume; Alviola et al., this volume).

The northern Sierra Madre have been known since the 1890s to harbor unique species of terrestrial mammals. The shrew-mouse *Crunomys fallax* was discovered in the low foothills adjacent to the Cagayan River valley in Isabela Province in 1896 (Thomas, 1898; Musser, 1982; Rickart et al., 1998). More recently, a new species of shrew mouse, *Archboldomys musseri,* was discovered in the 1990s on Mount Cetaceo, the third highest peak in the range (Danielsen et al., 1994; Rickart et al., 1998). A decade after that discovery, a series of field surveys on several mountain peaks along the northern Sierra Madre (Duya et al., 2007) led to the discovery of *Apomys sierrae*, confined to the northern Sierra Madre and Caraballo mountains (Alviola et al., this volume; Heaney et al., this volume). A subsequent survey of the Mingan Mountains in the central Sierra Madre (Balete et al., this volume) led to the discovery of *Apomys aurorae* and *A. minganensis* (Heaney et al., this volume) and apparently new species of *Archboldomys* and *Rhynchomys* (Balete et al., this volume; D. S. Balete, unpubl. data). These studies confirmed that most, and perhaps all, isolated mountain peaks on Luzon Island are unique centers of mammalian endemism and that the northern Sierra Madre (i.e., north of the Mingan Mountains) is one such center of endemism (Heaney et al., 1999, 2003, this volume; Heaney & Mallari, 2000; Balete et al., 2006, 2009, this volume; Duya et al., 2007; Alviola et al., this volume; Rickart et al., 2011).

In 2004 and 2005, we returned to Mt. Cetaceo to conduct surveys to obtain additional information about the ecology of *Apomys sierrae* and *Archboldomys musseri*, to determine whether additional endemic species are present and to consider the conservation needs of the area. We focused our effort on the montane and mossy forest on the mountain, because prior surveys on Luzon have shown that most local endemics are present above 1000 m. Although these data are limited, they are the first quantitative data on small mammals from montane and mossy forest in the northern Sierra Madre, including the recently discovered endemic species, in what is likely to be the most species-rich habitat for small mammals. In this paper, we present information on patterns of species richness, relative abundanee, and habitat associations of native small mammals from 1300 to 1550 m. We also report qualitative data for large mammals encountered during the survey.

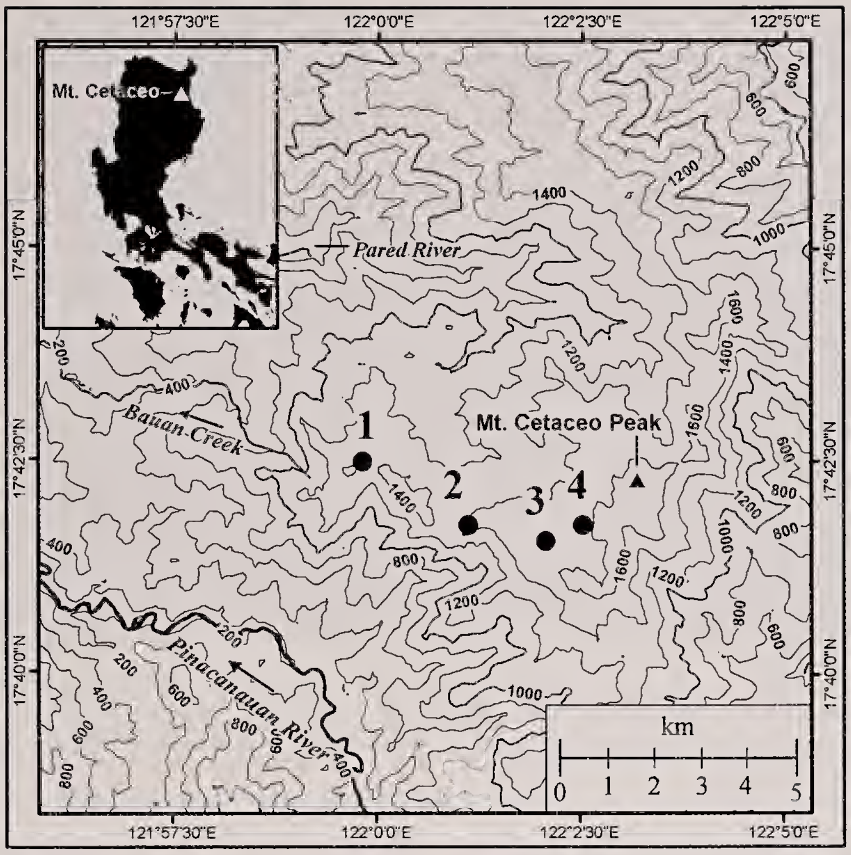

FIG. 1. Map of Mt. Cetaceo, with inset showing its location on Luzon. Sampling localities on Mt. Cetaceo are indicated by **solid circles**, numbered as in the list of study areas (see Methods). Contour interval = 200 m. Provided by Conservation International–Philippines.

Methods

Study Area

Mount Cetaceo (1730 m; Fig. 1; see also fig. 3 in Heaney et al., this volume), with its peak at 17.704594°N and 122.053244°E, is the third highest mountain peak in the northern Sierra Madre. The highest peaks are located south of Mt. Cetaceo in the provinces of Isabela and Aurora, with heights near 1850 m. Our survey was conducted in two field seasons (6–17 May 2004 and 7–19 June 2005) and was confined to the large tracts of montane and mossy forest along the western slope (Fig. 1) within Barangay Lapi, Peñablanca Municipality, Cagayan Province. The forest above 1000 m was relatively undisturbed, whereas the forest from about 700 to 1000 m was secondary lowland forest; below 700 m was a mixture of degraded lowland forest, slash-and-burn farms, grassland, and pasture areas. The 2004 survey was confined to lower montane forest at 1300 m, whereas the 2005 survey covered portions of the mountain between 1400 and 1550 m, encompassing upper montane and mossy forest. On the first field survey, we proceeded to Mt. Cetaceo on its western slope following an old logging road up to ca. 800 m elevation. Our survey area in lower montane forest at 1300 m was well above the lower margin of lower montane forest at ca. 1000 m. The second survey covered montane forest at 1400 m and mossy forest at 1500 and 1550 m, which we reached by the same route.

LOCALITY 1—0.4 km N, 6.0 km W of Mt. Cetaceo peak, 1300 m elev., 17.707934°N, 121.996988°E (6–17 May 2004). The lower montane forest at this location was dominated by *Tristaniopsis* sp. and *Lithocarpus* sp. with an average canopy height of ca. 10–12 m and average DBH (diameter at breast-height) of ca. 16 cm. Emergent trees, principally *Agathis philippinensis,* were approximately 20 m in height. Undergrowth included ferns, gingers, and palms (*Pinanga* sp.). Several species of rattan were abundant. *Selaginella* sp. and *Medinilla* sp. were common, and epiphytes were abundant, particularly orchids. Mosses were moderately common and forest litter was 3–5 cm deep. No disturbance was observed except for some active snares set by local people. Victor rat traps were set on the ground for a total of 824 trap-nights; no arboreal trapping was conducted.

LOCALITY 2—3.7 km WSW of Mt. Cetaceo peak, 1400 m elev., 17.69561°N, 122.01863°E (7–18 June 2005). This locality was situated along a ridge in montane forest. The prevailing canopy, ca. 7–10 m high, was dominated by *Tristaniopsis* sp. and *Lithocarpus* sp. with DBH of 5–10 cm. A few emergent trees were observed reaching ca. 20 m in height, the largest being almasiga (*Agathis* sp.) with DBH ca. 0.5 m. The terrain was undulating with steep slopes. Species of Myrtaceae, *Lithocarpus*, *Podocarpus*, and *Dacrycarpus* were abundant. The ground surface was covered with leaf litter ca. 3–5 cm in depth; ferns, mosses (including *Sphagnum* sp.), viney pandans (*Freycinetia*), pitcher plants, and orchids were common. No disturbanee was observed except for snares. We set Victor rat traps on the ground (890 trap-nights) and Museum Specials in arboreal locations (84 trap-nights).

LOCALITY 3—2.0 km SW of Mt. Cetaceo peak, 1500 m elev., 17.69264°N, 122.03446°E (14–18 June 2005). The habitat at this locality was old-growth mossy forest (Fig. 2), with two creeks that drain to the Pared River, northwest of Mount Cetaceo. Emergent trees, ca. 6–7 m in height, consisted mainly of *Leptospermum, Lithocarpus,* and *Dacrycarpus* spp. Canopy species included *Elaeocarpus* sp. and *Syzygium* sp. with DBH of 5–15 cm; average canopy height was ca. 5 m. Orchids and vines were common epiphytes. *Pandanus* sp. were uncommon, *Freycinetia* was relatively common, and *Ficus* sp. were absent. Pitcher plants (*Nepenthes* spp.) were common. The understory

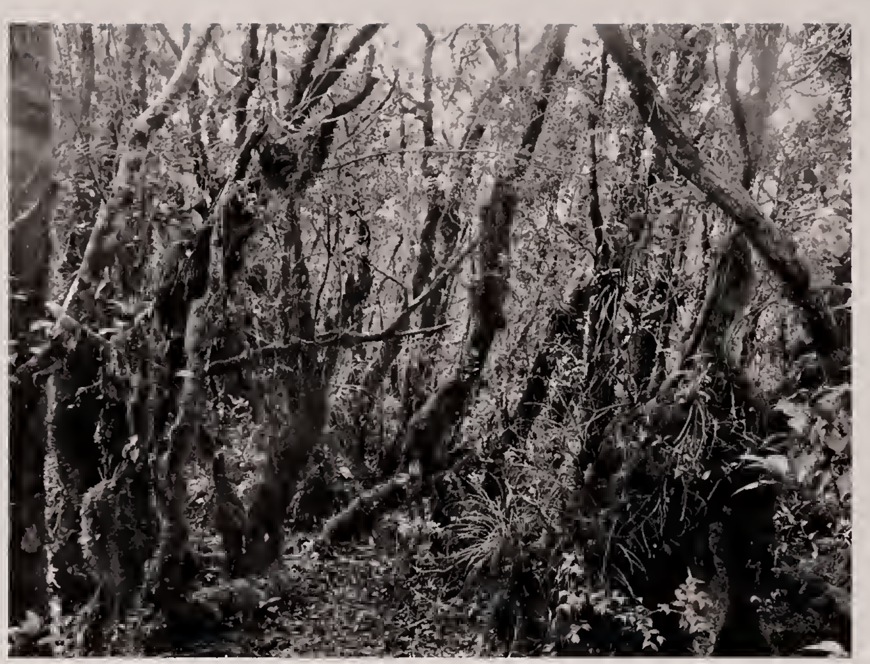

FIG. 2. Mossy forest habitat on Mt. Cetaceo at locality 3, 1500 m elevation. *Apomys sierrae* was abundant in this habitat, and *Archboldomys musseri* was present. June 2005, photographed by M. R. M. Duya.

was dominated by *Drymis piperata,* and ground cover by ferns and mosses. We set Victor rat traps on the ground (337 trap-nights) and Museum Special snap traps in arboreal locations (34 trap-nights).

LOCALITY 4—1.5 km SW of Mt. Cetaceo peak, 1550 m elev., 17.69579°N; 122.04216°E (16–18 June 2005). This locality was primary mossy forest, with prevailing canopy tree height of 4–5 m and consisting mainly of *Elaeocarpus, Syzygium, Gordonia, Weinmannia,* and *Leptospermum.* Emergent trees were dominated by *Lithocarpus*, *Pittosporum,* and *Dacrycarpus,* with an average height of 6–7 m. Undergrowth plants were dominated by *D. piperata* and ferns (*Asplenium* sp.), and pitcher plants (*Nepenthes* spp.) were common. Canopy epiphytes including *Vaccinium* sp., *Medinilla* sp., mosses, and orchids were common. *Freycinetia* sp. and *Alyxia* sp. were the most common vines in the area. Tree trunks were thickly covered with moss, and the ground surface was covered by a thick layer of leaf litter and moss. We set Victor rat traps on the ground (344 trap-nights) and Museum Specials in arboreal locations (59 trap-nights).

Field Methods

This survey followed the standard field methods employed in our previous surveys of Philippine small mammals to make data comparison possible (Heaney et al., 1989, 1999, 2006b; Rickart et al., 1991, 1993, 2011; Balete et al., 2009, this volume; Alviola et al., this volume). Traps were baited either with fried coconut coated with peanut butter or with live earthworms. Victor rat traps were set along runways, under root tangles, and on top of or alongside fallen logs. Museum Special snap traps were set on horizontal branches of trees, overhanging lianas, and vines. All arboreal traps were baited with fried coconut coated with peanut butter. Ground traps (Victor rat traps) comprised 93% of traps set, and arboreal traps (Museum Special snap traps) represented 7%; of 2395 trap-nights on the ground, 55% of traps were baited with coconut and 45% were baited with live earthworms. Trap lines were maintained for three to four consecutive days before being transferred to another site, except at locality 4, where traps were set for two days. Traps were serviced twice each day, in the early morning (ca. 0700 h) and in the afternoon (before sundown, ca. 1700 h), to retrieve captures and replace bait. Traps were set on ridge tops and along slopes and ridgesides to sample all available microhabitats. Animals retrieved at 0700 h were considered nocturnal captures, whereas animals retrieved at ca. 1700 h were noted as diurnal captures. All captured individuals of small mammals were preserved as voucher specimens, and identifications were verified at the Field Museum. A tissue sample taken from the thigh was placed in 95% ethyl alcohol or DMSO buffer solution before preserving the specimens. Specimens were injected with saturated formalin solution, then soaked in 10% buffered formalin (and later transferred to 70% ethanol) or prepared as complete skeletons. Nomenclature was based on Heaney et al. (1998, this volume). Specimens were deposited at the Field Museum of Natural History, Chicago (FMNH) for further study; a portion will be returned to the National Museum of the Philippines, Manila (NMP), after completion of our studies. The capture and handling of animals in the field was conducted in accordance with all relevant Philippine laws and regulations.

To gather data on large mammals, we interviewed local hunters and our guides using color photos, and we observed traps (e.g. *silo* or noose) set by local people, footprints, fecal droppings, nesting and roosting sites, and animal remains. Animals traded in nearby villages, especially those taken within the survey area, were also noted, and we questioned our informants regarding the extent of hunting, trapping, and other forms of gathering.

Data Analysis

The number of species recorded at a given locality was estimated as the number recorded directly plus the number presumed present because of their presence at localities above and below along the elevational gradient (e.g., Rickart et al., 1991). To measure the adequacy of sampling, we used species accumulation curves. For locality-specific assessment, we plotted the cumulative number of species captured against the number of trap-nights (defined as 1 trap set for 24 h) at each elevation. We also plotted a species accumulation curve for all four elevations combined, including all types of traps and baits, beginning at the lowest elevation and proceeding to the highest. This method has been used previously in the Philippines to assess the completeness of sampling effort for mammalian species richness (Rickart et al., 1991; Heaney et al., 1999, 2006a; Heaney, 2001; Balete et al., 2009, this volume; Alviola et al., this volume). Accumulation curves for large mammals were not constructed because effort in recording them was not standardized.

Trap success for each species at each elevation was derived by dividing the number of individuals of each species captured times 100 by the number of relevant trap-nights (i.e., the number of captures per 100 trap-nights). Bait preference of each species was derived in a similar manner, expressed as the value of the total captures per bait type times 100 divided by the relevant total of trap-nights for the bait. Weighted trap success, which we used as a measure of relative abundance of each species at each site, was calculated as the number of individuals captured times 100 divided by the total number of ground traps set. The unweighted (equalized) trap success was expressed as the average of each species' trap success for the two bait types used. χ^2 tests were used to determine whether

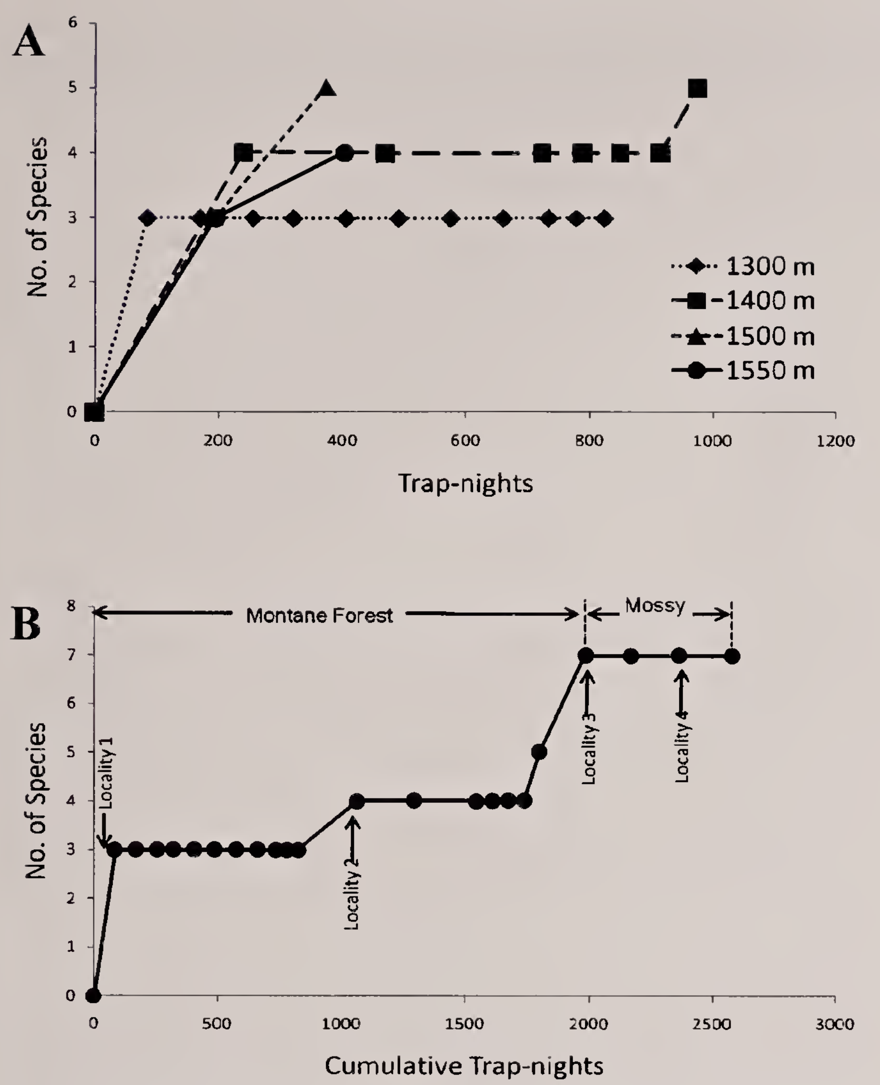

FIG. 3. Species accumulation curves for native non-volant small mammals on Mt. Cetaceo (**A**) in individual study areas and (**B**) for the entire transect, indicating the habitat type at each elevation.

differences were significant for habitat preference, bait type, and diel activity, with expected values calculated on the basis of the number of relevant trap-nights. For diel activity, the expected frequency was computed as the ratio 10:14, the proportion (in 24 h) of diurnal and nocturnal/crepuscular activity time periods. For all χ^2 tests, we followed the convention of conducting tests only on total samples of 20 or more individuals, with five or more individuals per "treatment" in at least 80% of the treatments (e.g., per elevation or bait type). Spearman's rank correlation was used to determine correlation between several variables (percent trap success with the 2 baits, overall trap success, and diel activity period) and elevation. With only four elevational samples, statistical significance by Spearman's rank correlation cannot be achieved, but we make note of strong trends when they are present.

Numerical estimates were not possible for large mammals; rather, we recorded only presence or absence. Data presented here are based on reports from local guides and hunters and our observations of signs (e.g., feces and wallows).

Results

A total of 2572 trap-nights (ground and arboreal traps) was set at the four elevations, resulting in the capture of 257 individuals of native small mammals (Table 1). This included six murid rodents (*Apomys microdon, A. musculus, A. sierrae, Archboldomys musseri, Bullimus luzonicus*, and *Rattus everetti*) and one shrew (*Crocidura grayi*). Although we documented the presence of the large murid rodent *Phloeomys pallidus* during the survey, we treat that species as a large mammal (ca. 2.5 kg) because it cannot be captured with standard traps used for small mammals. We also recorded the presence of deer (Cervidae: *Cervus mariannus*), wild pigs (Suidae: *Sus philippensis*), macaques (Cercopithecidae: *Macaca fascicularis*) and civets (Viverridae: *Paradoxurus hermaphroditus*).

Species accumulation curves for individual elevations did not reach a plateau, except in montane forest at 1300 m (Fig. 3A). The number of species recorded at 1300 m reached an asymptote after 85 trap-nights and continued until the end of the trapping period, whereas at 1500 and 1550 m, the number of species had not reached a plateau when the respective trapping periods ended at ca. 400 trap-nights. At 1400 m, a long plateau from ca. 500 to 950 trap-nights was followed by the capture of one additional species on the last day of trapping. The total cumulative number of species gradually rose to seven, with a short asymptote after 2000 trap-nights (Fig. 3B). This implies that few additional species might be expected within the elevational range of 1300–1550 m, but because of the limited elevational range (and correspond-

TABLE 1. Distribution of non-volant small mammals along the elevational transect on Mt. Cetaceo. Captures greater than expected from χ^2 tests are indicated in boldface. Numbers in parentheses are specimens caught in arboreal traps that are not included in the χ^2 test. Numbers in brackets are number of individuals/100 trap-nights. χ^2 values test for difference between pairs of montane (1300, 1400 m) and mossy (1500, 1550 m) forest localities.

Species	1300 m	1400 m	1500 m	1550 m	Total trapped	χ^2	*P*
Crocidura grayi	0	1 [0.11]	0[a]	1 [0.29]	2 [0.08]	—	—
Apomys sierrae	66 [8.01]	57 [6.40]	**33** [9.79]	**47** [13.66]	203 [8.48]	12.02	0.001
Apomys microdon	0	1 (1)	0	0	1 (1) [0.04]	—	—
Apomys musculus	0	0	(1)	0	(1)	—	—
Archboldomys musseri	0	0	2 [0.59]	2 [0.58]	4 [0.17]	—	—
Bullimus luzonicus	14 [1.70]	14 [1.57]	1 [0.29]	5 [1.74]	34 [1.42]	1.94	0.163
Rattus everetti	5 [0.61]	7 [0.79]	1	0	13 [0.54]	2.75	0.097
Total captures	85 [10.32]	80 [8.99]	**37** [9.30]	**55** [16.86]	257 (+2[b]) [10.73]	6.85	0.009
Total trap-nights (ground)	824	890	337	344	2395		
Total trap-nights (arboreal)	0	84	34	59	177		
Total no. of species	3	5	5 (+1[a])	4	7	—	—

[a] Presence inferred (see Methods).
[b] Individuals captured in arboreal traps.

TABLE 2. Summary of overall captures by bait type and diel period of all native non-volant small mammals on Mt. Cetaceo (see Table 1 for the breakdown of captures by species). Captures that are greater than expected with respect to bait type, as indicated by χ^2 tests, are shown in boldface. Relationship between percent success (no. of individuals/100 trap-nights) and elevation is indicated by Spearman's correlation, r_s.

	1300 m	1400 m	1500 m	1550 m	Total	r_s	P
Coconut bait							
Trap-nights	408	632	201	84	1325		
Captures	41	38	13	1	93		
% Success	10.04	6.01	6.47	1.19	7.02	−0.800	0.1646
Earthworm bait							
Trap-nights	416	258	136	260	1070		
Captures	44	**42**	**24**	**54**	**164**		
% Success	10.57	16.28	17.65	20.77	15.33	1.000	0.0818
χ^2	0.06	21.48	9.23	15.22	38.08		
P	0.814	<0.0001	<0.001	<0.0001	<0.0001		
Overall trap success (%)							
Weighted[a]	10.32	8.99	10.98	15.99	10.73	0.800	0.1646
Unweighted[b]	10.31	11.15	12.06	10.98	11.17	0.400	0.4840
Diel period							
Diurnal	0	1	3	6	10		
Nocturnal/ crepuscular	85	79	34	49	247		
% Diurnal	0	1.25	8.11	10.91	3.89	1.000	0.0818

[a] Percent success for all trap-nights.

[b] Mean of the percent ground trap success with coconut and worm baits.

ing habitat diversity) sampled, it does not imply that only seven species occur on the mountain.

A total of five species was recorded in montane forest (1300 and 1400 m) and six species in mossy forest (1500 and 1550 m; Table 1). The greatest number of species recorded or inferred (6) was present in mossy forest at 1500 m, and five were found in montane forest at 1400 m. Only three species (*A. sierrae, B. luzonicus*, and *R. everetti*) were captured in montane forest at 1300 m elevation. These species were also captured in transitional forest between lowland and montane forest at 960 m in a previous study conducted in the southwestern portion of Mt. Cetaceo with the use of cage and locally made snap traps (Duya et al., 2007).

Among the species captured, the most common was *A. sierrae,* with overall relative abundance of 8.48 individuals per 100 trap-nights for the entire survey. This was followed by *B. luzonicus,* with relative abundance of 1.42 per 100 trap-nights, and *R. everetti,* with relative abundance of 0.54 per 100 trap-nights. Some species of small mammals differed in abundance between montane and mossy forest (Table 1). *Apomys sierrae* was significantly more abundant in the mossy forest pair than in the montane forest pair. *Bullimus luzonicus* and *R. everetti* had too few captures to be tested statistically, but both appear to have been more abundant in montane than in mossy forest (Table 1). *Crocidura grayi*, *A. microdon*, and *A. musculus* were captured too few times to reliably estimate their relative abundances. Overall relative abundance of small mammals was greater in mossy forest than in montane forest; clearly, this was heavily influenced by the greater abundance of *A. sierrae* in mossy forest (Table 1). Similar levels of abundance have been documented in montane and mossy forest in other studies on Luzon (Balete et al., 2009, this volume; Alviola et al., this volume; Rickart et al., 2011).

Our data on bait preference by native small mammals show no significant difference in montane forest at 1300 m, but earthworm bait was highly preferred over coconut bait at all three higher elevations (Table 2). Percent trap success with earthworm bait was high at all localities and exhibited a strong trend to increase with increased elevation (by about a factor of 2); in contrast, we documented a strong trend toward a decrease in trap success with coconut bait with increased elevation (by about a factor of nearly 5). Overall trap success weighted by actual bait used tended to be correlated with elevation, but when we equalized bait types (i.e., used an unweighted measure), no such trend was present (Table 2). Only *A. sierrae* exhibited a significant bait preference (for earthworms; Table 3). *Bullimus luzonicus* and *R. everetti* did not show any significant bait preference, even though sample sizes were probably sufficient to detect statistical differences (Table 3). Other species had too few captures to reveal patterns of bait preference.

The percentage of diurnal activity showed a strong trend toward a positive correlation with elevation, increasing by about an order of magnitude along the gradient (from 0% to 11%; Table 2), with distinctly lower daytime activity recorded in montane forest than in mossy forest. *Apomys sierrae, B. luzonicus*, and *R. everetti* exhibited significant nocturnal/crepuscular activity (Table 3). We captured too few *C. grayi* or *A. microdon* to detect patterns of diel activity. Although only four *Archboldomys musseri* were captured, three of them were daytime captures, suggesting that species is active both day and night.

Our records of large mammals were based on interviews with our local guides and actual signs of, encounters with, or both during the field surveys. We encountered *Cervus mariannus* while setting our traps at locality 2. Several tracks of *Sus philippensis* were also observed between 1300 and 1550 m. Both species were heavily hunted in the area. This was evident from the presence of an active hunting camp at ca. 1350 m approximately 2 km from locality 1; according to the local hunters, they frequently used the camp when checking their snares once each week. One hunter claimed to have set 150 snares for wild pigs and deer and said he captured an average of three wild pigs every six months. He claimed to capture an average of two deer per year using the same snares.

TABLE 3. Summary of captures of six species of non-volant small mammals on Mt. Cetaceo by bait type and diel period. Percent trap success (number of individuals/100 trap-nights) is based on total ground traps (see Table 1) and is shown in brackets. Captures greater than expected from χ^2 tests are shown in boldface.

		Bait type		Diel activity	
Species	**Total**	**Coconut**	**Earthworm**	**Nocturnal/Crepuscular**	**Diurnal**
Crocidura grayi	2	1 [0.08]	1 [0.09]	2	0
Apomys sierrae	203	62 [4.68]	**141**[a] [12.18]	**196**[a]	7
Apomys microdon	1	1 [0.08]	0 0	1	0
Archboldomys musseri	4	1 [0.08]	3 [0.28]	1	3
Bullimus luzonicus	34	19 [1.43]	15 [1.40]	**34**[a]	0
Rattus everetti	13	9 [0.68]	4 [0.37]	**13**[a]	0

[a] $P < 0.01$.

In 2004, we encountered local hunters carrying an adult female deer captured in one of the snares they set at 1300 m, and our guides captured an adult male wild pig near our 1300-m study area. Local people told us that deer were getting harder to catch, whereas wild pigs were still relatively abundant.

We also encountered scat of the Malay civet (*Paradoxurus hermaphroditus*). We documented the slender-tailed cloud rat (*Phloeomys pallidus*) on two occasions. One was foraging on a tree along the trail at ca. 900 m, and two young individuals were brought to us by local people who said they caught them in a shallow cave near a corn field and were keeping them as pets. Although we did not observe any signs of long-tailed macaque (*Macaca fascicularis*), our local guides claimed that they were quite abundant in the lower elevations and considered them to be pests in corn plantations.

Discussion and Conclusion

Our data derive from four localities encompassing the montane and mossy forest on the western slope of Mt. Cetaceo; although clearly limited in elevational extent, this study represents the first standardized data on the small mammals of this distinctive center of mammalian endemism. We documented a total of seven species of nonvolant small mammals, with five species occurring in the montane forest (1300 and 1400 m) and six species in mossy forest (1500 and 1550 m; Table 1). It is worth noting that we captured only three species at 1300 m in spite of sampling effort greater than at 1500 and 1550 m, and that a previous study (Duya et al., 2007) documented the same three species at ca. 960 m in disturbed forest at a lower elevation on Mt. Cetaceo. This implies that species richness may increase along the elevational gradient, as found elsewhere on Luzon (Heaney, 2001; Balete et al., 2009; Rickart et al., 2011).

Given that the highest elevation on Mt. Cetaceo is 1730 m, our data from 1300 to 1550 m might not have captured all of the species present within montane and mossy forest on Mt. Cetaceo. Previous studies indicate that species richness usually peaks at the transition between montane and mossy forest, followed by a plateau or decline at higher elevations, but additional species sometimes occur only above this transition zone (Heaney, 2001; Heaney et al., 2006b; Balete et al., 2009; Rickart et al., 2011). We therefore suggest that additional standardized trapping be conducted from 1550 m up to the mountain peak at 1730 m to ascertain the adequacy of sampling in the area, as well as at lower elevations.

Our data indicate that overall relative abundance (calculated as weighted trap success; see Methods) shows a trend toward a positive correlation with increasing elevation (Table 1). *Apomys sierrae* was significantly more abundant in the mossy forest localities compared with the montane forest localities, and this species accounted for most of the increase in overall abundance. Relative abundance of closely related large-bodied *Apomys* showed similar increases in montane and mossy forest on Mts. Mingan, Tapulao, and Bali-it (Heaney, 2001; Balete et al., 2009, this volume; Rickart et al., 2011), but not on Mt. Palali (Alviola et al., this volume).

We found that trap success with roasted coconut bait tended to decrease with increasing elevation along our short transect, but trap success with earthworm bait tended to increase more rapidly with increasing elevation, leading to the slightly increased overall abundance noted above (Table 2). Much of this increase in success with earthworm bait was due to the increasing abundance of *A. sierrae* with increasing elevation and their significant preference for earthworm bait (Table 3). We also noted a significant increase in diurnal activity along the transect, from 0% in montane forest at 1300 m to 11% in mossy forest at 1550 m (Table 2). Both of these patterns are consistent with those observed previously on other elevational transects. It is interesting to note that *Archboldomys musseri*, an insectivore/vermivore species, exhibited mostly diurnal activity on the basis of our small sample, similar to *A. kalinga* and *A. luzonensis* (Rickart et al., 1991, 2011; Balete & Heaney, 1997) and in contrast to roughly equal diurnal and nocturnal activity shown by *Archboldomys* sp. from Mt. Mingan (Balete et al., this volume).

Comparison of the faunas from available transects on Luzon shows some commonalities among the native nonvolant small mammal assemblages. A few species have been found along nearly every transect, and all of these are present on Mt. Cetaceo: *Crocidura grayi*, *Apomys microdon*, *Bullimus luzonicus*, and *Rattus everetti*. All of them occur in lowland forest in many areas, perhaps explaining their wide distributions. *Apomys musculus* has been found on nearly every surveyed mountain with an elevation over about 1700 m. Individual species of large-bodied *Apomys* (such as *A. sierrae*) have limited geographic distributions, but taken together, these animals (members of the subgenus *Megapomys*; Heaney et al., this volume) occur widely over large portions of central and northern Luzon above about 600 m, so their presence on Mt. Cetaceo is not surprising. We have recently discovered species of *Archboldomys* over wide areas on Luzon, always on mountains with elevations greater than 1700 m, but they are absent from the Zambales Mountains (Balete et al., 2009) and probably some other areas (Alviola et al., this volume), so the presence of an apparently endemic species on Mt. Cetaceo is noteworthy.

The apparent absence of some taxa on Mt. Cetaceo is also noteworthy. The murid genera *Batomys, Carpomys, and Rhynchomys* have been found only on mountains with peaks reaching about 1900 m or higher. Species of *Rhynchomys* have been found on Mts. Tapulao, Mingan, Isarog, Bali-it, and Banahaw (peak = 2177 m), and *Carpomys* has been documented only in the Central Cordillera (with a maximum elevation of ca. 2900 m, including Mt. Bali-it at 2150 m), whereas *Batomys* species have been found only in the Central Cordillera and on Mt. Isarog (1966 m). The absence of these genera from Mt. Cetaceo can be attributed in part to its low elevation and the associated reduced variety and area of habitat. We do not expect that the mammal fauna on Mt. Cetaceo represents the entire high-elevation fauna of the northern Sierra Madre because several other peaks in the region are higher, but these data suggest that these three "missing" genera might not be present in the northern Sierra Madre and are consistent with the hypothesis that elevation plays a role in determining species richness and assemblage composition of nonvolant small mammals in a given area (Heaney & Rickart, 1990; Heaney, 2004; Rickart et al., 2011). We recommend that additional field surveys be conducted on the highest peaks in the northern Sierra Madre, including the top of Mt. Cetaceo, to ascertain the presence or absence of genera such as *Batomys*, *Carpomys*, and *Rhynchomys* that occur only at the highest elevations.

The presence of *Archboldomys musseri* on Mt. Cetaceo and of *Crunomys fallax* in the lowlands of the Sierra Madre in Isabela Province, and the widespread distribution of *Apomys sierrae* as an endemic species in the northern Sierra Madre and the adjacent Caraballo Mountains indicate that the northern Sierra Madre is an area of endemism, distinct from other such faunal regions on Luzon (Rickart et al., 1998, 2011; Duya et al., 2007; Alviola et al., this volume; Heaney et al., this volume). Further studies along more complete portions of the elevational gradient and on higher peaks within the northern Sierra Madre are needed to determine whether still more endemic species are present.

Our data on large mammals suggest that the species were still relatively abundant in the area and inhabited both the lowland and montane forest of Mt. Cetaceo. However, on the basis of our interviews, Philippine brown deer (*Cervus mariannus*), Philippine warty pigs (*Sus philippensis*), palm civets (*Paradoxurus hermaphroditus*), giant cloud rats (*Phloeomys pallidus*), and long-tailed macaques (*Macaca fascicularis*) were actively exploited for food. Giant cloud rats and long-tailed macaques were considered to be agricultural pests and often hunted or taken as pets. To maintain stable populations of all of these species, hunting should be regulated, and the local people should be educated about proper management and the importance of these species in maintaining forest ecosystems. The montane and mossy forest of Mt. Cetaceo was not under threat at the time of our study, thus providing protection for endemic species of small mammals such as *Archboldomys musseri and Apomys sierrae*, but lowland forest was rapidly being converted to agriculture, adding to the threat facing large mammals. To ensure the continuous survival of these species, the montane and mossy forest and the remaining lowland forest of Mt. Cetaceo must be protected from future disturbance.

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Chapter 5: Enhanced Sampling of Bat Assemblages: A Field Test on Mount Banahaw, Luzon

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Abstract

We used a combination of capture methods—harp traps, a tunnel trap, and mist nets—to sample the bat assemblage at two locations (disturbed lowland forest at 620 m and old-growth montane forest at 1450 m) on Mount Banahaw, Luzon Island, Philippines. We placed harp traps and mist nets on ridges and across trails and streams in ravines. The tunnel trap was placed over streams. Over 13 nights, we captured 300 individuals representing 23 species, including two possibly undescribed rhinolophid species. Seventy percent of all mist net captures were frugivores (family Pteropodidae), 95% of harp trap captures were members of the narrow-space insectivore ensemble (the families Rhinolophidae and Hipposideridae and the vespertilionid *Kerivoula whiteheadi*), and 89% of all bats captured in the tunnel trap were edge-and-gap insectivores, comprising vespertilionids, excluding the subfamily Kerivoulinae. In the lowland forest location, harp traps set along a ridge captured 10 times as many bats as an equal number of harp-trap-nights in a nearby valley. The rapid accumulation of individuals and species over only 13 nights, and effective sampling of insectivorous bats of the families Rhinolophidae, Hipposideridae, and Vespertilionidae, including several poorly known species, indicate that the methods used in this study may be used successfully to further our knowledge of tropical bat assemblages.

Introduction

Tropical bats are highly diverse both taxonomically and ecologically, and despite a growing number of studies, many aspects of their ecology and taxonomy are poorly known. They comprise one-third of all mammal species in mainland Southeast Asia (Francis, 2008). In the Philippines, a total of 78 species have now been documented, comprising almost 38% of native terrestrial mammal species (Heaney et al., 1998, 2003, 2010; Esselstyn et al., 2004; Duya et al., 2007; Helgen et al., 2007). Bats provide ecosystem services such as seed dispersal (Fleming & Heithaus, 1981; Utzurrum, 1995; Shilton et al., 1999; Ingle, 2003), pollination (Start & Marshall, 1977; Kress, 1985; Mayfield et al., 2006; Nakamoto et al., 2009), including many mangrove species and the commercially important durian (Smith et al., 1992; Bumrungsri et al., 2009), and predation on insects, including crop pests (Leelapaibul et al., 2005). Colonies of cave-roosting insectivorous bats can contain millions of individuals; guano deposits, which are commercially important as fertilizer, are indicators of the high biomass of insects that bats consume (Lee & McCracken, 2005; Leelapaibul et al., 2005; Cleveland et al., 2006).

From a conservation perspective, the relatively long life spans, low reproductive output (1 or 2 young per year), and colonial roosting of cave-roosting bats and flying foxes (Pteropodidae) make bats particularly susceptible to population declines from direct persecution and habitat disturbance or loss. Furthermore, in identification of key areas for conservation attention, species lists often provide the only basis for assigning species' threatened status and prioritizing localities for protection, given the absence of population size data for most species (Polasky et al., 2000; Loiselle et al., 2003). Notwithstanding their taxonomic, ecological, commercial, and conservation importance, tropical bat assemblages are notoriously difficult to survey thoroughly. Unlike birds, their closest ecological analogs, bats cannot be effectively observed visually. With the exception of Old World frugivores, they emit high-frequency echolocation calls that can be surveyed with the use of ultrasonic detectors. Ultrasonic detectors are particularly useful for surveying high-flying bat species, which tend to produce loud high-intensity echolocation calls (Kalko, 1995; McCracken et al., 2008). But the accurate identification of calls to species can be problematic (Barclay, 1999), especially in the tropics where comprehensive libraries of calls are generally unavailable. However, even when calls are clearly species-specific, species with high-frequency, low-intensity calls (e.g., small hipposiderids and species within the vespertilionid subfamilies Kerivoulinae and Murininae) could be difficult to detect at more than a few meters away (Kingston et al., 1999).

Therefore, most bat sampling methods must involve capture, but the diversity of foraging, commuting, and sensory strategies exhibited by bats makes it impossible to sample all species effectively with a single method. The most common, and often the only, method employed for surveys of bats is mist netting (e.g., Heideman & Heaney, 1989; Patterson et al., 1996; Sampaio et al., 2003). Appropriately placed mist nets effectively capture primarily frugivorous bats: phyllostomids in the neotropics (e.g., Bonaccorso, 1978; Kalko et al., 1996; Medellin et al., 2000; Bernard & Fenton, 2003; Sampaio et al., 2003) and pteropodids in the paleotropics (e.g., Ingle, 1993; Francis, 1994; Juste & Perez del Val, 1995; Sedlock et al., 2008). Understory insectivores are generally underrepresented, and it is presumed that their echolocation call design (adapted for cluttered environments) enables them to detect and evade mist nets. Moreover, nets are often set only at ground level, but bats fly at different heights (Ingle, 1993; Francis, 1994; Bernard, 2001). Harp traps, which consist of a set of banks of fine wires or monofilament lines strung on a frame with a collecting bag below, are much less detectable to many echolocating bats and have proven extremely effective in capturing understory insectivores, especially in the paleotropics (Francis, 1989, 1990; Kingston et al., 2003; Struebig et al., 2006; Sedlock et al., 2008), but fail to sample larger, higher-flying bats. Tunnel traps, which consist of a large enclosure of netting suspended in the forest and with an open side that is closed upon entry of a bat, have opened a window onto the world of fast-flying edge-and-gap insectivores (Sedlock, 2001; Sedlock et al., 2008) but are less effective at capturing bats that do not use large flyways, such as rivers and streams. Moreover, the microhabitat in which each method is used could influence the number and type of bats captured (Kunz & Kurta, 1988; Duffy et al., 2000). Clearly, no single method is effective for studying tropical bat assemblages. As a result, the species richness and relative abundance of species reported may more accurately reflect the method(s) used, rather than the actual composition and structure of the bat assemblage sampled.

Philippine bats provide a good example of the knowledge-bias that can result from single-method bat inventories. Decades of mist net studies have amassed considerable data on fruit bat diversity (Heaney, 1991), foraging ecology (Utzurrum, 1995, 1998; Ingle, 2003), elevational distribution (Heaney et al., 1989; Ruedas et al., 1994), demography (Heideman & Heaney, 1989), reproductive biology (Heideman, 1989; Heideman et al., 1993), biogeography (Roberts, 2006a), and population genetics (Roberts, 2006b). In contrast, published studies focused on insectivorous bats are few (Rickart et al., 1989; Sedlock, 2001, 2002; Sedlock et al., 2008; Sedlock & Weyandt, 2009), and we have almost no information on habitat use, diet, and other aspects of their ecology. A systematic approach to bat sampling with the use of several capture methods must be employed in the Philippines (and elsewhere) if we are to understand the role of different bat species in the forest community, know the archipelago's true biological value, and use the most effective approach to preserve it.

At two localities within Mount Banahaw–San Cristobal National Park, Luzon, we tested the relative effectiveness of mist nets, four-bank harp traps, and a tunnel trap in capturing bats that employ different foraging strategies. We also compared the relative effectiveness of harp traps placed along ridge trails compared with those set along trails in valleys. This study represents the first intensive inventory of the bat assemblage within the park.

Materials and Methods

Study Areas

Our study was conducted on southern Luzon Island within Mt. Banahaw–San Cristobal Park, Tayabas Municipality, Quezon Province (peak at 2130 m, 14°04′2.38″N, 121°29′32.31″E; see Heaney et al., this volume, fig. 3). We sampled bats at two locations on the southern slope of Mt. Banahaw between 16 and 29 August 2004:

"LOWLAND FOREST" LOCALITY—5.1 km E, 2 km S Mt. Banahaw peak, 620 m elevation, 14°03′06.5″N, 121°32′22.5″E. At this locality, we sampled along a ridge trail through a narrow strip of regenerating lowland forest adjacent to clearings planted with agricultural crops, including sweet potato (*Ipomoea batatas*), taro (*Colocasia esculenta* and *Xanthosoma sagittifolium*), cassava (*Manihot esculenta*), bananas (*Musa* spp.), and coconut (*Cocos nucifera*). Bamboo and other grasses were also abundant. We also sampled along the Alitao River and its tributaries in a river valley covered with disturbed second-growth lowland forest. The forest canopy was ca. 25 m, with emergents rising up to ca. 35 m, comprised mainly of dipterocarps (Dipterocarpaceae) and members of Elaeocarpaceae and Myrtaceae. Canopy vines including lianas, climbing bamboo (*Dinochloa*), jade vines (*Strongylodon macrobotrys*), and climbing pandan (*Freycinetia*) were abundant. Large epiphytic ferns (*Asplenium*), orchids, and flowering vines (*Medinilla*) were common up on the big trunks and high branches of canopy trees. Along the river banks, tree ferns, ground ferns, and gingers (Zingiberaceae) were also common.

"MONTANE FOREST" LOCALITY—1.7 km E, 0.4 km S Mt. Banahaw peak, 1453 m elevation, 14°03′59.1″N, 121°30′30.7″E. This locality was situated in old-growth montane forest. Two small streams ran through the study area. The forest canopy at these elevations was ca. 12–15 m, with emergents rising to about 20 m. Dominant trees included species of *Podocarpus* (Podocarpaceae), *Lithocarpus* (Fagaceae), and *Syzygium* (Myrtaceae). Mosses, liverworts, epiphytic ferns, orchids, and the epiphytic shrub *Medinilla* were abundant on tree trunks and branches. Understory vegetation included erect palms (*Pinanga*) and tree ferns (*Cyathea*). Vines including rattan (*Calamus*) and climbing pandan (*Freycinetia*) were common in the forest. Along river banks, lianas, tree ferns (*Cyathea*), and gingers (Zingiberaceae) were common.

Bat Sampling

We conducted field research in the lowland forest locality between 16 and 21 August 2004 and in the montane forest locality between 22 and 29 August 2004. We used harp traps, a tunnel trap (Sedlock, 2001), and mist nets. Four-bank harp traps (width = 1 m, height = 1.5 m, strung with 0.22-mm-diameter monofilament lines 2.5 cm apart and offset between banks) were placed along trails and, occasionally, along narrow creek beds. Traps were checked at least every half hour between 1830 and 2200 h and then checked periodically throughout the night. Harp traps were moved to a new location every night. A "trap-night" represented one harp trap left open all night for one night.

At the lowland forest locality, harp traps were set in two general locations: across a trail along a ridge (16–18 August 2004) and across trails in a nearby valley with small creeks (19–21 August 2004), for a total of 15 harp-trap-nights each. At the montane forest locality, harp traps were set across a ridge trail for a total of 25 trap-nights (24–28 August 2004) and across trails and small streams in the nearby valley for a total of 10 trap-nights (22–23 August 2004). Harp trapping resulted in 30 and 35 trap-nights at the lowland and montane localities, respectively.

The tunnel trap consisted of a large enclosure (height = 5 m, width = 5 m, length = 10 m) of nylon netting set along a river at each sampling locality (Sedlock, 2001). The netting on one side was hoisted up to allow entry of bats, and the trap was continually tended by one or two persons, who closed the open side as soon as a bat was detected inside. The bat was then captured with a hoop net. A fluorescent lamp was placed inside the trap to attract insects and facilitate detection of bats. The tunnel trap was opened at dusk and serviced until 2100 h. Tunnel trapping occurred on three nights along one river at the lowland forest locality and four nights at the montane forest locality—two nights each at two rivers.

Mist nets were set at ground level and as high nets (i.e., 2 or 3 nets stacked one on top of the other; Ingle, 1993). Mist nets were opened at dusk and checked at least every half hour until at least 2200 h and then periodically throughout the night. Nets were closed during rain, and therefore those nights were excluded from the netting effort. A net-night was equivalent to one 6-m net (height = 2.6 m, 38 mm mesh) open from dusk to early the next morning; thus two 12-m nets stacked one on top of the other represented four net-nights. Mist nets were set in three different microhabitats: across streams, in tree-fall gaps, and on ridges. At the lowland forest locality, two 12-m mist nets were set, one on top of the other, across a dry stream, and two 6-m nets were set, one on top of the other, in a tree-fall gap. At the montane forest locality, we tended one 12-m net across a stream over four nights for a total of eight net-nights, and three sets of two 6-m stacked nets along the ridge over four nights for a total of 24 net-nights. Mist-netting efforts resulted in 12 and 32 net-nights at the lowland and montane forest localities, respectively.

We recorded the sex, age, reproductive condition, mass, and forearm length of all captured bats. We marked captured bats by trimming a patch of fur on the forehead to enable identification of recaptures. Any recaptures were immediately released and are not included in the results. Bats were identified to species using Ingle and Heaney (1992). Bat species were classified into three foraging strategies on the basis of their diet and echolocation call design following the classification scheme of Schnitzler and Kalko (1998). All fruit-eating pteropodids were classified as frugivores. The large open-space "flying foxes" were not included in this study. Insectivorous rhinolophids, hipposiderids, and species in the genus *Kerivoula* use echolocation strategies that eliminate or minimize call-echo overlap, allowing them to forage for prey within dense vegetation. We refer to these species as "narrow-space insectivores." All vespertilionids with frequency-modulated call sweeps lasting greater than 5 ms, which limits prey detection in dense vegetation, were classified as "edge-and-gap insectivores."

We collected up to 10 individuals per species as voucher specimens. Total length, tail length, foot length, and ear length were measured on voucher specimens. Tissue samples were taken from all sacrificed bats and preserved in 95% ethanol. Voucher specimens were deposited at the Field Museum of Natural History (FMNH) in Chicago for taxonomic study. Half of these specimens will be returned to the Philippines and be housed at the Philippine National Museum in Manila. All Philippine laws and regulations were followed in the conduct of this research.

To assess the comprehensiveness of sampling and to compare species accumulation rates among localities and sampling methods with unequal sampling effort, Coleman curves were calculated with EstimateS (Colwell, 2004). Coleman curves were sample-based, and sample order was randomized 100 times to smooth the curve. Accumulation curves were generated separately for lowland and montane forest localities to better meet the assumption of habitat homogeneity.

Results

Three hundred individual bats representing 23 species were captured (Table 1). These included two species of *Rhinolophus* that may represent undescribed species. *Rhinolophus* sp. A resembled *Rh. arcuatus* in external and skull measurements and echolocation call but differed with respect to nose leaf morphology and cytochrome *b* sequences (Sedlock & Weyandt, 2009). *Rhinolophus* sp. B and *Rh. virgo* both had noseleaves with a notched connecting process and were similar to each other with respect to forearm length (Table 1); however, *Rhinolophus* sp. B had larger ears and a larger anterior noseleaf than *Rh. virgo*. Moreover, the peak frequency (i.e., frequency with the most energy) of the echolocation call of *Rhinolophus* sp. B was lower in frequency than that of *Rh. virgo*. *Rhinolophus* spp. A and B were captured sympatrically at the lower elevation site along a single ridge with *Rh. arcuatus* and *Rh. virgo*, respectively.

Despite greater trapping effort over all methods at the montane forest locality, the lowland forest locality yielded more than twice as many individuals and species. Fifteen species were caught only in the lowland forest locality (Table 1), including all hipposiderids, and two were caught only in the montane forest locality (*Miniopterus tristis* and *Myotis rufopictus*). Among fruit bat species found in both localities, *Otopteropus cartilagonodus* was most numerous in the montane forest locality and *Ptenochirus jagori* in the lowland forest locality. *Rhinolophus arcuatus* was the most commonly captured species at both localities, accounting for 29% of all captures. *Rhinolophus* sp. A was the second most frequently captured species in the lowland forest locality but was not captured in the montane forest locality.

Mist nets accounted for 21% of the total individuals captured, representing 11 species; harp traps accounted for 63% of total captures, representing 18 species, and the tunnel trap yielded 16% of the total captures, representing nine species. The tunnel trap captured an average of seven individuals per tunnel-night, followed by harp traps (5.2 individuals/harp-night) and mist nets (1.4 individuals/net-night).

The majority (70%) of mist net captures were frugivores, whereas harp trap captures were dominated by narrow-space insectivores (95%) and tunnel trap captures by edge-and-gap insectivores (89%) (Fig. 1). Two frugivore species were caught exclusively in mist nets (*P. jagori* and *Rousettus amplexicaudatus*). All but seven of the 187 rhinolophids and hipposiderids captured, representing 11 species, were taken only in harp traps. The exceptions were singletons of the largest hipposiderid, *Hipposideros diadema*, and the largest rhinolophid, *Rhinolophus inops*, and five *Rh. arcuatus*. *Philetor brachypterus* was caught only in the tunnel trap.

The shape of species accumulation curves differed with capture method and locality (Fig. 2). By reading the Coleman curves from left to right, one can compare the cumulative

Table 1. Bats captured on Mt. Banahaw in lowland forest and montane forest on 16–29 August 2004, indicating capture methods, with method yielding most captures for each species capitalized. Forearm length range (mm) is for adults only.

	Lowland 620 m	Montane 1450 m	Capture method[a]	Forearm (n)	Guild[b]
Pteropodidae					
Cynopterus brachyotis	7		M, h	60.2–75.2 (3)	f
Macroglossus minimus	3		M, h	40.1–40.5 (2)	f
Otopteropus cartilagonodus	4	22	M, h, t	44.2–47.1 (17)	f
Ptenochirus jagori	11	1	M	74.7–79.9 (6)	f
Rousettus amplexicaudatus	1		M	75.8 (1)	f
Hipposideridae					
Coelops hirsutus	4		H	34.4 (1)	nsi
Hipposideros ater	1		H	41.0 (1)	nsi
H. bicolor	1		H	43.7 (1)	nsi
H. diadema	2		H, t	83.0 (1)	nsi
H. obscurus	8		H	43.9–46.6 (5)	nsi
Rhinolophidae					
Rhinolophus arcuatus	47	40	H, m, t	35.5–49.1 (74)	nsi
Rh. macrotis	2		H	45.6–45.7 (2)	nsi
Rh. inops	14	1	H, m	52.8–56.0 (12)	nsi
Rh. virgo	12		H	38.2–41.6 (12)	nsi
Rhinolophus sp. A	43		H	39.5–48.6 (38)	nsi
Rhinolophus sp. B	2		H	39.2–40.4 (2)	nsi
Vespertilionidae					
Kerivoula whiteheadi	6	5	H, t	28.4–32.9 (10)	nsi
Miniopterus tristis		8	M, t	51.7–55.7 (8)	egi
Myotis horsfieldii	12		T, h	35.2–37.7 (12)	egi
My. muricola	5		T, m	31.2–32.9 (5)	egi
My. rufopictus		2	h, m	47.7–51.2 (2)	egi
Philetor brachypterus	5		T	34.5–37.1 (4)	egi
Pipistrellus javanicus	7	24	T, h, m	31.7–35.9 (30)	egi
Total species	21	8			
Total individuals	197	103			
Harp-nights	30	35			
Mist-net-nights	12	32			
Tunnel-nights	3	4			

[a] h, harp trap; m, mist net; t, tunnel trap.

[b] egi, edge-and-gap insectivore; f, frugivore; nsi, narrow-space insectivore.

number of species captured for a given sampling effort by the different sampling methods. Given equal harp- and net-nights, harp traps accumulated more species (11 total) than nets (5) at the lowland forest locality. Conversely, nets accumulated more species (7) than harp traps (3) at the montane forest locality after equal sampling effort. In lowland forest, three tunnel-nights resulted in the same number of species as three harp-nights (5) and more species than three net-nights (3). In montane forest, four tunnel-nights yielded more species than four harp- or net-nights. Species accumulation curves suggested that harp trap, tunnel trap and mist net sampling were incomplete in both the lowland and montane forest localities, given that the accumulation curves did not reach a plateau.

At the lowland forest study area, with equal harp-trapping effort along the ridge and in the valley, the ridge traps captured almost 10 times as many rhinolophids as those in the valley and about twice the number of species (15 in ridge, 8 in valley; Fig. 3). Overall, ridge traps captured an average of 8.5 bats/trap-night, whereas valley traps captured 1.1 bats/trap-night. In the montane forest locality, we did not have equal numbers of traps along the ridge and in the valley, and the capture rates were higher in valley traps, with a ridge average capture rate of 0.8 bats/trap-night (over 25 trap-nights) and a valley rate of 1.9 bats/trap-night (10 trap-nights).

Discussion

Using three capture methods for bats (mist nets, harp traps, and a tunnel trap) over two weeks of fieldwork at two localities on Mt. Banahaw, we documented 309 individuals of 23 species of bats, of which 84% were insectivores (Table 1). In contrast, previous studies in the Philippines using only mist nets resulted in captures dominated by frugivores. In fact, L. R. Heaney et al. (unpubl. data) sampled bats using mist nets at the same two localities as the present study in April 2004 and captured only fruit bats. At the montane forest locality (9 nights, 18 net-nights) they captured nine fruit bats (all *O. cartilagonodus*), and at the lowland forest locality (3 nights, 18 net-nights) they captured 40 fruit bats representing four species (*Cynopterus brachyotis*, *Macroglossus minimus*, *O. cartilagonodus*, *R. amplexicaudatus*). We mist-netted all these fruit bat species during our study (Table 1), plus *P. jagori*.

Similarly, over 680 net-nights on Mt. Isarog in southeastern Luzon Island, Heaney et al. (1999) captured 304 individual bats representing 18 species; 74% of the individuals captured were frugivores (6 species) and only 26% were insectivores (12 species). Revisiting six of the same localities on Mt. Isarog, Sedlock et al. (2008) captured 709 individuals representing 26 species, using a combination of mist nets (275 net-nights), harp

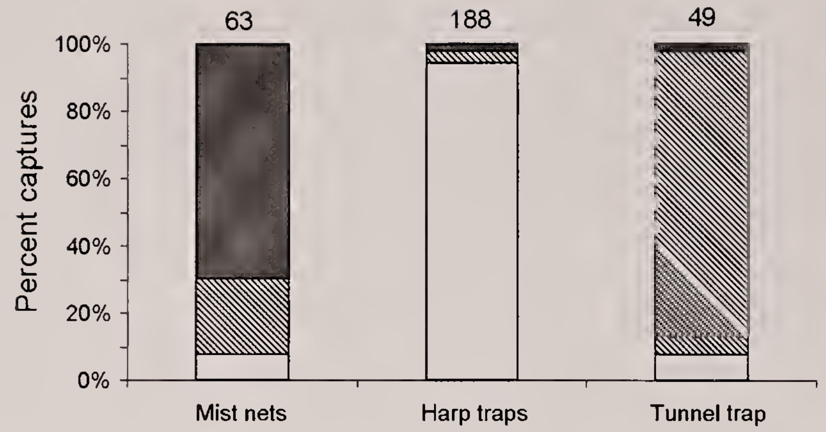

FIG. 1. Composition by foraging strategy of bats captured using mist nets, harp traps, and tunnel trap: frugivores (**shaded**), edge-and-gap insectivores (**hatched**), and narrow-space insectivores (**white**). Sample sizes given above bars.

traps (397 trap-nights), and a tunnel trap (29 tunnel-nights). Of the bats captured, 65% were insectivores (21 species) and 35% were frugivores (5 species). This comparison also illustrates the trade-off between allocating the available field effort across multiple capture methods or concentrating effort on one method (e.g., mist nets). By doubling their mist net effort, Heaney et al. (1999) caught a relatively rare fruit bat species, *Harpyionycteris whiteheadi* (n = 3), that was missed by Sedlock et al. (2008). However, the multimethod sampling approach of Sedlock et al. (2008) yielded not only more species of insectivorous bats, but considerably more individuals. For example, Heaney et al. (1999) captured only four individuals of *Rhinolophus arcuatus*, whereas it was the most commonly captured species (in harp traps) in the 2008 study. Therefore, for a rapid and thorough survey of bat assemblages, using a combination of capture methods is dramatically more effective than mist nets alone in numbers of individuals and species captured (Francis 1989, 1990; Sedlock et al. 2008). The difference results from the behavior of insectivorous species, which are poorly sampled with mist nets. For additional bat capture methods, see Francis (2008).

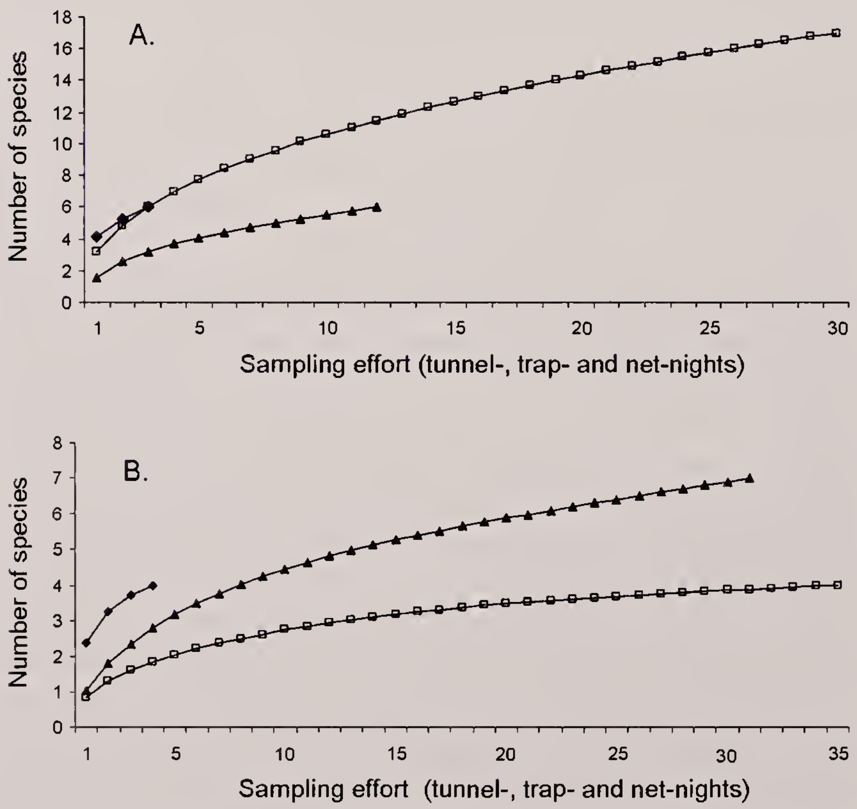

FIG. 2. Species accumulation in (**A**) lowland and (**B**) montane forest on Mt. Banahaw as a function of capture effort using harp traps (**open squares**), mist nets (**filled triangles**), and a tunnel trap (**filled diamonds**).

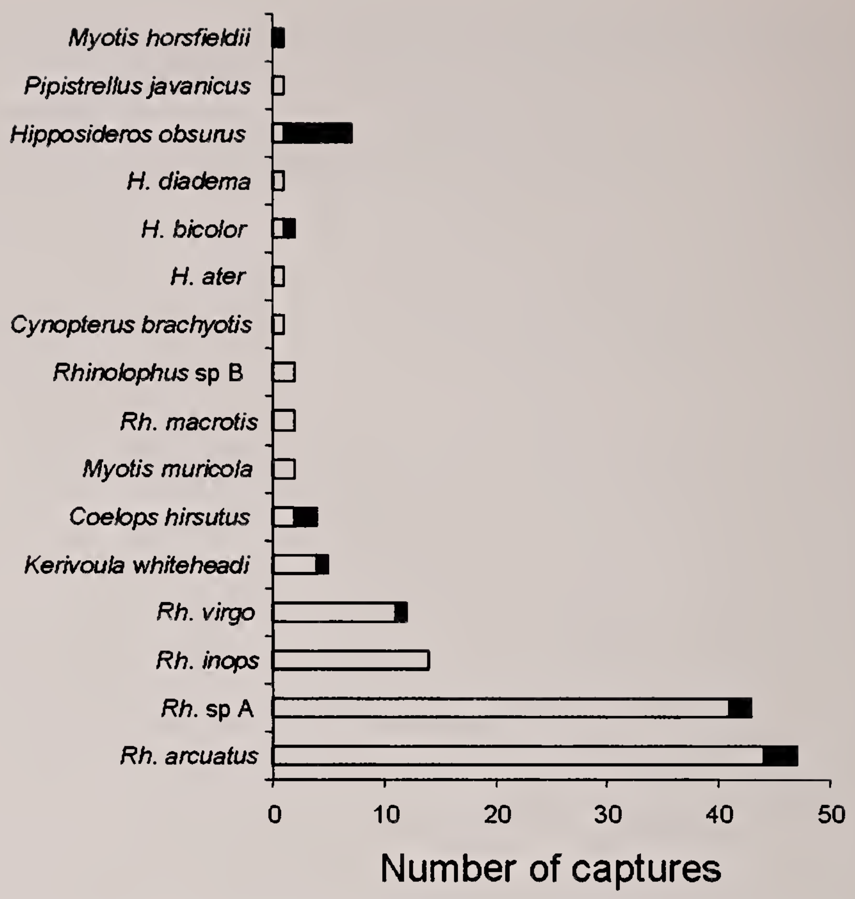

FIG. 3. Number of harp trap captures along the ridge (**white**) and in the valley (**black**) at the lowland forest locality over 15 trap-nights per microhabitat.

The three capture methods we employed revealed strikingly different views of the bat assemblage present within Mt. Banahaw–San Cristobal National Park. Harp traps captured almost exclusively narrow-space insectivores, the tunnel trap captured primarily edge-and-gap insectivores, and mist nets captured predominantly frugivores (Fig. 1). The assemblage composition and structure resulting from employing multiple capture methods was more species-rich and evenly distributed across foraging guilds than presented in previous studies relying solely on mist nets.

Microhabitat influenced capture success in harp traps (Fig. 3). At the lowland forest locality, we set an equal number of harp traps at the same height above ground along a ridge trail bounded by dense vegetation and in the valley where trails were not as pronounced. Capture rates of the ridge traps were an order of magnitude higher than the valley traps. In the montane forest site, harp traps in the valley captured about twice as many bats on average as those along the ridge. We have no replicates (i.e., 1 ridge and 1 valley per locality), so the dramatic difference in capture success in lowland forest could be due to factors unassociated with microhabitat, such as the proximity of a cave roost to the ridge that was sampled. We suspect, however, that high capture rates in the ridge traps in the lowland forest locality was because the opening formed by the trail coupled with the dense vegetation bounding it made it a very effective flyway. In contrast, the valleys did not have pronounced trails.

Harp traps in this study captured several individuals of species either previously not recorded on Luzon Island or known from only a few records. For example, we captured four individuals of *Coelops hirsutus*, a small understory hipposiderid. Previously known from only a few records (Heaney et al., 1998), *C. hirsutus* was listed as "data deficient" on the IUCN Red List (IUCN 2009). Given that it has since been documented with harp traps on Mt. Makiling and Mt. Isarog on Luzon (Sedlock et al., 2008), it appears that *C.*

hirsutus is common where present, and not currently threatened. Similarly, before the use of harp traps in the Philippines, *Kerivoula whiteheadi* was known only from one locality on Luzon Island (Isabela Province) and thought to be restricted to lowlands. This study and a harp trap study on Mt. Isarog (Sedlock et al., 2008) revealed that *K. whiteheadi* was relatively common and ranged from lowland to upper montane forest (ca. 1450 m elevation). The genus *Kerivoula* is represented by eight species in peninsular Malaysia (Kingston et al., 1999, 2003; Francis et al., 2007) and Indonesian Borneo (Struebig et al., 2006), where harp traps have been employed extensively. Increasing use of harp traps in the Philippines might reveal additional species in the genus.

The tunnel trap is a relatively new method but has proved invaluable in the rapid documentation of fast-flying edge-and-gap insectivores (Sedlock, 2001). In this study, *Philetor brachypterus* would have gone undetected without the use of a tunnel trap, and only a few individuals of other insectivores, such as *Myotis horsfieldii* and *Miniopterus tristis*, would have been captured.

Conclusion

A bat survey using a combination of mist nets, harp traps, and a tunnel trap was successful in rapidly documenting frugivores, narrow-space insectivores, and edge-and-gap insectivores on Mt. Banahaw. Bat studies employing these methods simultaneously and systematically in the Philippines and elsewhere in the tropics will surely open a window onto the structure of bat assemblages and provide more reliable estimates of species distributions and population status. The harp trap and tunnel trap are effective capture techniques for many insectivorous bat species that have been unrepresented in bat studies. They also have the potential to contribute to the effectiveness of another method for sampling insectivorous bats, acoustic monitoring, which requires a "call library" from captured bats from the same geographic populations to identify calls to species (e.g., Kalko, 1995).

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